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BOOK REVIEW

TRAUGOTT-OLSEN, E. and E. SCHMIDT NEILSEN. 1977. 'The Elachistidae (Lepidoptera) of Fennoscandia and Denmark'. Scandinavian Science Press Ltd. Klampenborg, Denmark. 299 pages.

This is a frustrating text because it contains more information than is usually presented in a general handbook, but less than one might expect in a revision.

However, the nine introductory sections provide an excellent basis for understanding the treatment of elachistine genera and species found in northern Europe. Structure of adults and immatures is described and all characters used in the text are described and figured. The position of the family Elachistidae within the Gelechioidea is discussed and the family diagnosed. A generic phylogeny is presented, and status of questionable genera is explained. There are brief sections on bionomics, zoogeography, and nomenclature.

The remaining seven sections of text consist of keys to genera and species, and descriptions of taxa known to occur in the area covered. This part of the book is well organized, as are the keys, which contain very few ambiguous couplets. Where possible, keys for larvae are also presented. Descriptions are detailed and uniform in presentation, with short sections covering biology, distribution, and major synonymies. Unfortunately, the authors chose not to point out diagnostic characters in species descriptions, so that while keys are sufficient for identification purposes, differences between closely related species are not readily appreciated from the descriptions, and even less so in the keys. This could be confusing if the descriptions are to be used in conjunction with the keys, and it is certainly confusing to the reader.

The figures are generally clear and sharp, although the presentation of larval mining patterns is less than satisfactory. These are presented as half-tone pencil drawings which makes details in many of them difficult to perceive. Simple line drawings would have presented these patterns much more clearly. Scales are not given on the plates, but Figures 1 through 152 are stated to be approximately 5.5 times

magnification. Figures 153 through 536 are without indication of magnification, as are all text figures.

Distributional data are not well presented, and are dealt with only superficially. There are no distribution maps, although, with considerable effort, they could be constructed from data presented. This is an area where treatment is weak and where the synthesis falls short of that which might be expected in a revision of the group. In defense of the authors, a catalogue arranged by species and province is presented in which records are shown by a full or half dot. However, no indication is given of the significance of the two symbols used. A half dot appears to be used where two provinces are combined in the catalogue and appear to represent presence in one, but not in the other; there is a 50 percent chance of guessing correctly. No precise locality data are presented, and type localities are not mentioned. Biogeography is treated very superficially.

Although a generic phylogeny is presented, species relationships are not discussed beyond broad species groups in the largest genus. Little attempt is made to discuss trends in structure or bionomics.

The text is generally free of errors.

If you are interested in Fennoscandian Elachistidae, this is a reasonably good text; if you are not, there is little here for you. If this review seems harsh, it is simply because the authors have missed a number of opportunities to synthesize their data more completely, and thus make the work more valuable to those outside a rather restricted field of interest.

E.M. Pike
Department of Entomology
University of Alberta
Edmonton, Alberta, Canada
T6G 2E3

STONEFLIES (PLECOPTERA) OF SASKATCHEWAN

LLOYD M. DOSDALL¹

Biology Department
University of Saskatchewan
Saskatoon, Saskatchewan
S7N 0W0

D.M. LEHMKUHL

Biology Department
University of Saskatchewan
Saskatoon, Saskatchewan
S7N 0W0

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Forty-one species, twenty-nine genera and eight families of Plecoptera are recorded from Saskatchewan. Distinguishing characters are given and keys are provided. Species recorded are: Pteronarcys dorsata (Say), Pteronarcella badia (Hagen), Taeniopteryx nivalis (Fitch), Oemopteryx foscetti (Ricker), Capnia coloradensis Claassen, Capnia confusa Claassen, Capnia gracilaria Claassen, Capnia vernalis Newport, Paracapnia angulata Hanson, Isocapnia crinita (Needham and Claassen), Isocapnia missouri Ricker, Utacapnia trava (Nebeker and Gaufin), Nemoura rickeri Jewett, Shippa rotunda (Claassen), Amphinemura linda (Ricker), Zapada cinctipes (Banks), Malenka californica (Claassen), Podmosta delicatula (Claassen, Paraleuctra vershina Gaufin and Ricker, Leuctra ferruginea (Walker), Acroneuria abnormis (Newman), Acroneuria lycorias (Newman), Hesperoperla pacifica (Banks), Claassenia sabulosa (Banks), Paragnetina media (Walker), Perlesta placida (Hagen), Isoperla bilineata (Say), Isoperla longiseta Banks, Isoperla transmarina (Newman), Isoperla patricia Frison, Isoperla decolorata (Walker), Isoperla marlynia Needham and Claassen, Isoperla petersoni Needham and Christensen, Arcynopteryx compacta (MacLachlan), Skwala parallela (Frison), Isogenoides colubrinus (Hagen), Isogenoides frontalis (Newman), Diura bicaudata (Linnaeus), Triznaka signata (Banks), Suwallia lineosa (Banks) and Hastaperla brevis (Banks). Nymphs of the following ten species are described for the first time: Oemopteryx foscetti, Triznaka signata, Suwallia lineosa, Isoperla decolorata, Nemoura rickeri, Malenka californica, Podmosta delicatula, Capnia coloradensis, Capnia confusa, and Capnia gracilaria. Keys to species are provided for mature nymphs except that nymphs of Isocapnia crinita and Isocapnia missouri are unknown, and nymphs of Malenka californica and Amphinemura linda are inseparable, as are nymphs of Capnia coloradensis from Capnia confusa and Isogenoides frontalis from Isogenoides colubrinus.

The following information is presented for each species: selected literature references, diagnostic information, bionomics, and distribution which consists of a brief summary of the species range and a map showing Saskatchewan collection localities. Diagnostic illustrations are provided.

Life history patterns and seasonal succession of Saskatchewan stoneflies are discussed. Life cycles range from more than one year to univoltine. Some species with a one-year life history diapause as embryos, others do not. The post-glacial dispersal of stoneflies to Saskatchewan is discussed.

¹Present address: P.O. Box 7415, Saskatoon, Saskatchewan, S7N 4J3

Integration of the geographical and ecological distributions of extant species with the post-glacial history of Saskatchewan leads to the inference that the Saskatchewan stonefly fauna is derived mainly from post-glacial dispersal from refugia to the south and northwest of the Wisconsin ice sheets.

Quarante et une espèces de Plécoptères se rencontrent en Saskatchewan. Ces espèces se distribuent en huit familles et 29 genres. L'adulte de chaque espèce est caractérisé, et nous pourvoyons une clef permettant leur identification. Les espèces de cette région sont: Pteronarcys dorsata (Say), Pteronarcella badia (Hagen), Taeniopteryx nivalis (Fitch), Oemopteryx foscetti (Ricker), Capnia coloradensis (Claassen), Capnia confusa (Claassen), Capnia gracilaria Claassen, Capnia vernalis Newport, Paracapnia angulata Hanson, Isocapnia crinita (Needham et Claassen), Isocapnia missouri Ricker, Utacapnia trava (Nebeker et Gaufin), Nemoura rickeri Jewett, Shipsis rotunda (Claassen), Amphinemura linda (Ricker), Zapada cinctipes (Banks), Malenka californica (Claassen), Podmosta delicatula (Claassen), Paraleuctra vershina Gaufin et Ricker, Leuctra ferruginea (Walker), Acroneuria abnormis (Newman), Acroneuria lycorias (Newman), Hesperoperla pacifica (Banks), Claassenia sabulosa (Banks), Paragnetina media (Walker), Perlesta placida (Hagen), Isoperla bilineata (Say), Isoperla longiseta Banks, Isoperla transmarina (Newman), Isoperla patricia Frison, Isoperla decolorata (Walker), Isoperla marylnia Needham et Claassen, Isoperla petersoni Needham et Christensen, Arcynopteryx compacta (MacLachlan), Skwala parallela (Frison), Isogenoides colubrinus (Hagen), Isogenoides frontalis (Newman), Diura bicaudata (Linnaeus), Triznaka signata (Banks), Suwallia lineosa (Banks) et Hastaperla brevis (Banks). Nous décrivons pour la première fois les stades nymph aux des espèces suivantes: O. foscetti, T. signata, S. lineosa, I. decolorata, N. rickeri, M. californica, P. delicatula, C. coloradensis, C. confusa et C. gracilaria. Nous pourvoyons une clef des espèces pour les nymphes au dernier stade, excepté pour cells d'I. crinita et d'I. missouri qui ne nous sont pas connues. De plus les nymphes des espèces paires suivantes ne peuvent être separees: le M. californica, d'A. linda, le C. coloradensis de C. confusa, et l'I. frontalis d' I. colubrinus.

Pour chaque espèce nous présentons les données suivantes: une série de references choisies, un diagnostic des stades, des notes sur la bionomique, et une distribution décrite brievement dans le texte et illustrée en detail sur une carte de la Saskatchewan. Nous avons illustré tous caractères structuraux d'importance.

Nous discutons pour les Plécoptères de la Saskatchewan les patrons d'histoire naturelle et de succession saisonnière. Le cycle vital s'étend sur une année (univoltine) ou plus (multivoltine). Quelques unes des espèces univoltines ont une période de diapause au stade d'embryo, les autres espèces ne l'ont pas. Nous discutons la dispersion post-glaciale des Plécoptères de cette région. L'integration des données écologiques et géographiques des espèces présentes avec l'histoire post-glaciale de la Saskatchewan suggere que la faune des Plécoptères s'est dispersée après les temps glaciaux à partir de refuges au sud au nord-ouest des glaciers partir de refuges au sud au nord-ouest des glaciers de la période du Wisconsin.

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INTRODUCTION

Introductory background and objectives of the study

Plecoptera, or stoneflies, are a small order of aquatic insects with approximately 2,000 species known in the world, and 470 species recognized from America north of Mexico. Stoneflies comprise a significant part of many lotic ecosystems, and to a lesser extent some lentic ecosystems. The nymphal stage forms an important link in the aquatic food web between the algal-detrital and vertebrate trophic levels. Also, nymphs have potential importance as indicators of water quality. Specific identification as well as knowledge of the distribution and way of life of stoneflies is a preliminary requirement to their use as indicators in assessment of water quality and to understanding dynamics of aquatic communities of which they are a component.

Studies of Plecoptera in Western Canada have largely excluded Saskatchewan. Banks (1907) reported species known from Alberta and British Columbia and Neave (1929, 1933, 1934) published records for several species from Alberta, British Columbia and Manitoba. Needham and Claassen (1925) listed one species from Saskatchewan. Ricker (1943) published a thorough study of the stonefly fauna of southwestern British Columbia and later (1944, 1946, 1965), published records of prairie and northern stoneflies including nine species from Saskatchewan. Cushing (1961) reported two species, from Montreal River, not previously known in the province. Records for these 11 species were from fewer than 10 Saskatchewan localities. It was evident, with the tremendous diversity and number of habitats represented in Saskatchewan, that a varied and extensive fauna should occur in the province. Lotic systems are well represented, especially in the boreal part of the province and, to a lesser extent, in the prairies and Cypress Hills regions.

This study of Saskatchewan Plecoptera had three main objectives. The first objective was to document nymphal as well as adult stages. Although adults of North American stoneflies are well known, less attention has been given to taxonomic characters of the nymphs. For many species, only mature nymphs with underlying adult characters can be definitely recognized at present, though the nymph is the stage of life cycle most commonly encountered in the field. Keys presented in this study, especially for immature stages of Plecoptera, will be useful for future ecological studies.

The second objective was to infer possible sources for the Saskatchewan stonefly fauna by examining their known North American distributions. Until this study, little could be stated of the post-glacial stonefly dispersal to Saskatchewan. Also, distributional information recorded here will be useful in assessing the effects of man's future alterations of Saskatchewan's rivers and streams.

The third objective was to summarize published information on life-cycles and to synthesize this with observations made on the way of life of Saskatchewan stoneflies.

A total of 41 species are known from Saskatchewan, including 30 new records for the province and four new Canadian records. New descriptions are presented for nymphs of ten species.

Morphology

The following text describes basic morphological characters of Plecoptera and is summarized from Hitchcock (1974) Gaufin *et al.* (1972), Merritt and Cummins (1978) and others.

Plecoptera are hemimetabolous, belonging to the orthopteroid group of insects. They are most closely related to Embioptera (Crampton, 1932, Nutting, 1951).

The eyes are generally posterior on the head, but in some species they are placed far forward. A few species have only two lateral ocelli, the majority have three: two lateral and one median with an imaginary or "ocellar triangle" connecting the three ocelli. The Y-shaped ecdysial line forks just posterior to the lateral ocelli. The posterior part of the head, or occipital region, may bear short bristles or long setae forming an occipital ridge.

The mouthparts are of the chewing type, though they are reduced in some adults. Nymphal mandibles may have grinding surfaces or be sharply toothed, depending on feeding habits (Fig. 166). Maxillary appendages include the 5-articled palpus, galea, and laciniae (Fig. 165). Laciniae may have one or two sharp teeth and a row or tuft of bristles. The labium bears a 3-articled palpus and two pairs of lobes distally, the outer paraglossae and inner glossae. Glossae and paraglossae are approximately of equal length in *Filipalpia* (Fig. 21), but in *Setipalpia* the glossae are much reduced and in some genera appear only as small projections on the inner side of the paraglossae (Fig. 20). There is a small mentum proximal to the labium, and beyond it a larger submentum (Fig. 20).

The pronotum may have a median longitudinal stripe or a reticulate pattern. The basisternum is the largest thoracic sternal sclerite and this is preceded by the small presternum and followed by the furcastrum (Fig. 18, 19). On each side of the furcastrum are the furcal pits and in certain species they are joined by a transverse ridge with another ridge posterior to each pit forming a Y-shaped line when they join and run together (Fig. 24, 25).

Nymphal fore and hindwing pads may be aligned at an angle (Fig. 14), or they may be subparallel with forewing and hindwing pads in line with each other (Fig. 15).

Adult wing venation shows little variation from the basic form. Except for three North American species, hindwings always bear an enlarged lobe in the anal region. Forewings can have up to three anal veins, with the second anal vein forked in some species. Generally, there is only one anal cell although several anal cells occur in some species. The number and position of crossveins, the point of origin and the degree of upturn of the first branch of the radial vein are important systematic characters.

Brachypterous individuals show distorted venation.

Many nymphs have gills on various parts of the body. Submental gills are small and finger-like arising from the posterior corners of the submentum (Fig. 20). Cervical gills on the neck may be simple (Fig. 11) or branched (Fig. 12). Thoracic gills may also be simple or branched. Some species have simple coxal gills occurring singly on the ventral surface of each coxa (Fig. 13). Abdominal gills occur laterally on basal abdominal segments (Fig. 6, 7), and subanal gills occur between the cerci. Except for coxal gills, larval gill remnants are visible on the adult.

Males bear various genitalic processes, used in mating, and which are important taxonomically. These projections range from small, hardly perceptible processes, to very elongate projections. The male genitalia generally consist of a median epiproct or supra-anal process (an unpaired structure attached to the tenth tergum) which can be simple (Fig. 93), complex (Fig. 50, 51), or not readily visible; there are sclerotized paragenital plates at its base. In some species additional processes occur at the base of the epiproct. Paraprocts are located on each side of the epiproct and can range in structure from being simple and fingerlike (Fig. 117, 118) to complex structures (Fig. 120). The seventh, eighth or ninth sternite have vesicles or basal lobes in some species (Fig. 62, 64) and the ninth sternite may have a heavy knob or "hammer" (Fig. 9). Recurved pointed hooks or "genital hooks" can emerge as paraprocts (Fig. 102) or as part of the tenth tergite (Fig. 8).

The relatively simple female abdomen has the seventh or eighth sternum produced to form a subgenital plate (Fig. 116).

Single-, or many-articled cerci arise from the tip of the abdomen, and may bear characteristic bristles or hairs.

Economic importance of Plecoptera

Stoneflies are economically important mainly as natural fish food. A few fish species known to eat stoneflies include grayling (*Thymalus arcticus*), (Rawson, 1950), lake sturgeon (*Acipenser fulvescens*), (Magnin and Harper, 1970), yellow walleye (*Stizostedion vitreum*), (Rawson, 1956) and mooneye (*Hiodon tergisus*) (Glenn, 1975). In Saskatchewan, adults of *Malenka californica* were found in stomachs of brook trout (*Salvenius fontinalis*), (D. Larson, pers. comm.).

Stoneflies also provide a significant food source for some birds. Hamilton (1933) noted that the winter stonefly *Allocapnia recta* constituted an important food source for five species of passerine birds. In Saskatchewan, *Pteronarcys dorsata* nymphs have been found in crops of the Common Merganser (H. Stelfox, pers. comm.).

Generally stoneflies are restricted to well-oxygenated, unaltered streams and so have been used as indicators of water purity. Roback (1974) examined 23 species of stoneflies and found that none occurred in dissolved oxygen concentrations of less than four parts per million (ppm.), alkalinity greater than 1000 ppm., or chloride greater than 1000 ppm. Gauvin (1958) found that fewer stonefly species occurred in the zone of degradation than in the zone of clean water in a polluted stream, and none were found in extremely polluted water.

Taenionema pacifica is a minor pest in orchards in the Pacific Northwest. It has been reported feeding on foliage, buds and fruit of apricots, peaches and plums (Newcomer, 1918, 1933).

Claire and Phillips (1968) observed nymphs of *Hesperoperla pacifica* attacking and killing eggs and alevins of rainbow trout (*Salmo gairdneri*) and cut-throat trout (*Salmo clarki*). However, Nicola (1968) found that scavenging by stonefly nymphs (*Alloperla* sp.) on dead salmon eggs was beneficial since it prevented the spread of fungal infestation to living eggs.

Macy and Bell (1968) found that *Hesperoperla pacifica* was an alternate intermediate host to an internal parasite of birds. Hall and Groves (1963) noted that cercariae of seven of nine trematode

species harboured in river snails entered nymphs of *Hesperoperla pacifica*.

The study area

The limits of the study area were the political boundaries of Saskatchewan. Battle Creek in Cypress Hills was most easily accessible for collecting near Reesor Lake, Alberta, about one-half mile west of the Saskatchewan border. Battle Creek flows east into Saskatchewan, and since stoneflies collected here undoubtedly occurred in Saskatchewan also, species collected near Reesor Lake were considered part of the Saskatchewan fauna.

Saskatchewan encompasses a wide range of vegetational, climatic and geological zones. Two of the major North American vegetational zones are represented in the province: Grassland in the semi-arid climate of the southwest, and Boreal Forest in the subhumid north (Coupland and Rowe, 1969).

The southern Grassland zone is mainly higher than 600 meters above sea level and composed of extensive till and lacustrine plain overlaying Cretaceous rock (Richards, 1969). The major drainage basin in the Grassland region is the extensive Saskatchewan River System composed of the North and South Saskatchewan Rivers which unite near the edge of the Boreal Forest zone to form the Saskatchewan River. The flow is to the northeast, eventually into Hudson Bay. The Saskatchewan River System is fed both by prairie surface runoff and by snowmelt near its source in the Rocky Mountains resulting in a definite water flow regime (Raby and Richards, 1969). Relatively low winter flows are followed by a rise in early spring when there is snowmelt in the prairies and foothills. After a spring peak, flow tends to decrease but rises again in May-June because of meltwater runoff from the Rocky Mountains. Declining flow leads to low flows in August and September with an even base-flow maintained in winter months.

In the southwestern corner of Saskatchewan, rolling plains gradually rise to the Cypress Hills uplands which reach a maximum elevation of 1393 m, the highest in the province. The highest parts of Cypress Hills are believed to have been unglaciated (Richards, 1969). Battle Creek, which flows through some of the highest Cypress Hills elevations, and Frenchman River which flows down the eastern slope of Cypress Hills, are the two prominent rivers of this area.

The Boreal Forest zone, mostly between 365 and 550 m above sea level, is an area of lakes, bogs, coniferous and mixedwood forest and rock outcrop. In the far north, east of Lake Athabasca, is subarctic lichen-woodland of open coniferous forest and reindeer moss. Extending southward to the Churchill River System is the northern coniferous forest of spruce and pine underlain mainly by Precambrian rock. To the south of the Canadian Shield, soils deepen over sedimentary rock and spruce, pine and poplar are abundant. The southern edge of the Boreal Forest is the aspen belt, transitional between Boreal Forest and Grassland. It is composed mainly of deciduous trees and a variety of shrubs and grasses on rich grey-black soils (Coupland and Rowe, 1969).

On the Shield much of the drainage flows southward to the Churchill River System or to Lake Athabasca in the northwest. Northeastern drainage is primarily to Reindeer Lake and Wollaston Lake. In the Boreal Forest zone, practically any depression in the bedrock is occupied by a lake, bog, or marsh. Streams and rivers are numerous and because of climate and other factors, water levels fluctuate far less than in the south.

MATERIALS AND METHODS

Collection sites

Many areas of the province were collected extensively. These included Cypress Hills, the Saskatchewan River System and much of the boreal forest region. Collecting trips to rivers and creeks

in southcentral and southeastern Saskatchewan produced no specimens so this area was sampled only superficially. In addition, access roads are poor or nonexistent in the northeastern (north of Southend, Sask.) and northwestern (north of Buffalo Narrows, Sask.) parts of the province, so collections are meagre from these areas. Extensive collecting in this far northern region may lead to new provincial records and certainly will modify some of the distributions presented here.

Collection and preservation of specimens

Stonefly nymphs were most commonly collected with a sweep net where one stirs up the river substrate with the feet while walking backward against the current. Stonefly nymphs which had been dislodged from the rocks were carried by the current into the net. The net content was examined for stoneflies by placing it in a white pan with water in the bottom.

Another collection method was simply to examine such submerged objects as rocks or logs by hand-picking and to remove any stoneflies present. Mature final-instar nymphs were collected from rocks close to shore where they had crawled to emerge. The latter method was ideal for streams too small to use the sweep net in, but was less productive than sweeping in larger, more swiftly flowing rivers. Cast skins were found under bridges, on rocks near streams, or on vegetation which borders streams. Nymphs and cast skins were preserved in 70-90 percent alcohol.

In order to rear nymphs for associations with known adults, they were transported to the laboratory in glass bottles or Nalgene plastic bottles containing river water. Since the survival rate of Plecoptera was higher when kept cool, these containers were placed in an ice chest during the period of transit. Periodic oxygenation with a battery operated airpump or replacement of the water in the container with fresh water was necessary on long trips.

Adults were collected by rearing mature nymphs in laboratory aquaria, by sweeping vegetation near streams with an aerial net or by examining bridges, posts, or tree trunks near flowing water. Some adults hide under rocks near the shore and were collected by turning over the rocks. Winter stoneflies (*Capnia*, *Oemopteryx*, *Taeniopteryx*, *Utacapnia*) were collected in large numbers on the snow and ice of river banks, or on bridges. Adults of *Paracapnia* were collected by throwing panfuls of water onto the riverbank. In a few minutes the adults were flooded out of cavities in the ground and were collected with forceps. Although a few species are known to come to light traps, such equipment was not used in this study. Since stoneflies are weak fliers, finding adults was often more difficult than capturing them.

Adults were preserved in 70-90 percent alcohol. Specimens of certain species changed color in alcohol. Adults of *Hastaperla* and *Suwallia* which were bright yellow in life, and *Triznaka* which were green, faded to white when preserved.

Rearing

Rearing nymphs to adults was necessary in order to associate the immature and adult stages of the life cycle. Two methods were used: the first was similar to that described by Smith (1975). An aquarium with dimensions of 1.7 x 0.3 x 0.3 m was filled with cold tap water and dechlorinated using two drops per gallon of a sodium thiosulfate solution (700 grams sodium thiosulfate per liter of water). The water was vigorously aerated, and cooled somewhat by running tap water through glass tubing in the bottom of the aquarium.

Plastic sheets of dimensions 29 cm x 45 cm were suspended from the edge of the aquarium just above the surface of the water. These sheets contained several holes, into which the rearing containers were fitted (Fig. 16). Rearing containers were made from sections of Nitex screening, with a 0.33 mm mesh size glued together to form a tube. A circular piece of screening glued to the lower end of the Nitex tube formed the bottom and a piece of plastic tubing covered with Nitex screening formed the lid

(Fig. 17). The rearing container was then fitted through a hole in the plastic sheet but the upper portion rested on top of the sheet. A mature nymph placed in the container was able to crawl up the screening and out of the water when emerging. The lid prevented escape of the adult. In instances where it was necessary to rear nymphs which were not mature, the appropriate food could be placed in the container with the nymph. Detritivorous species were given dead leaves which had soaked for months in water; carnivorous species were supplied with larval mayflies, caddisflies or other stoneflies.

Rearing of stonefly nymphs which emerge in early spring required temperatures in aquaria of about 1 C to 5 C, much colder than were possible in the apparatus just described, which was kept in a laboratory at room temperature. The second rearing method used was similar to the one described by Sawchyn (1971). Containers with nymphs in them were kept in a Sherer-Gillet controlled-environment cabinet with temperature and photoperiod controls. Temperatures could be maintained within ± 1 C of the desired level and the fluorescent lights were controlled by timers. The rearing chambers each consisted of an outside plexiglass vessel measuring 28 x 18 x 10 cm, each holding 15 containers. The cylindrical containers had a frame of plexiglass and were covered with a plastic screening of 8 meshes per cm. The cylinders were suspended in the vessel by wires so that there was sufficient room for mature nymphs to crawl out of the water to emerge. Plastic petri dishes (#1007), placed over the chamber tops, prevented escape of adults. Dechlorinated tap water was used, and aeration was provided by a Model 120 Silent Giant pump.

Clearing of genitalia

It was unnecessary to clear genitalia of Plecoptera in order to observe taxonomic details. Abdominal sclerites of some specimens were contracted when preserved in alcohol, but after placing the abdomen in KOH at room temperature for 5–6 hours, the contracted sclerites were gently pulled apart. This enabled more efficient examination of the genitalia.

Material examined and its disposition

Material examined in this study was based primarily on collections made during the spring and summer of 1974 and 1975 with a few specimens collected in 1976.

In addition, I have examined Saskatchewan material from the personal collections of Drs. D.M. Lehmkuhl and D.J. Larson, Mr. D.H. Smith, and Mr. Ron Demaray. I have also examined some material collected from Stoney Rapids and Black Lake by Mr. L. Kratt and from the Churchill River and Cluff Creek in the collections of the Saskatchewan Research Council.

I was unable to collect either males or females of certain species, but I was usually able to borrow missing specimens from the personal collection of W.E. Ricker for drawings.

Small representative collections of Saskatchewan Nemouridae and Perlidae were sent to R.W. Baumann (Brigham Young University, Provo, Utah) and to B.P. Stark (Mississippi College, Clinton, Miss.), respectively. The Churchill River and Cluff Creek collections remain with the Saskatchewan Research Council. Most of the remaining specimens from other sources have been returned to their collectors. The remainder of the material is in my collection.

Illustrations

Line drawings, prepared using the camera lucida, and photographs using the Zeiss Tessovar photographic unit, are presented to illustrate taxonomic keys and augment descriptions. Illustrations of homologous structures in related species are from the same aspect.

Terms

Most terms for insect structures are based on the usage of Snodgrass (1935). Those specific to Plecoptera are from Needham and Claassen (1925), Frison (1935, 1942), Ricker (1943, 1949, 1952, 1959, 1965), Hanson (1946) and Ricker and Ross (1969). The nomenclature for wing venation follows the system proposed by Comstock and Needham (1898-1899). The section on Morphology (page six) provides a discussion of some of the taxonomically useful characters and includes some explanation of the most important terms.

Verification of species identifications

With the exceptions of *Perlesta placida* (Hagen) and *Isoperla marlynia* Needham and Claassen, all species described in this study have been verified. However, since these two species are particularly distinctive, there is little doubt that my identifications are correct. R.W. Baumann of Brigham Young University, Provo, Utah verified the Nemouridae, and W.E. Ricker of the Fisheries Research Board of Canada, Nanaimo, B.C. confirmed the remainder of the species identifications.

Organization of family, genus and species accounts

The systematic arrangement used for all taxa is that of Illies (1966) and Zwick (1973). A systematic list of Saskatchewan stoneflies is presented in Table 1. Descriptions of each family and genus represented in Saskatchewan are presented after the keys. Information for these descriptions was obtained from Needham and Claassen (1925), Claassen (1931), Frison (1935, 1942a), Ricker (1943, 1952), Gaufin *et al.* (1972) and Hitchcock (1974) as well as from my collections.

For genera with more than one species known from Saskatchewan, a key to adults is provided, and keys to nymphs are given where possible.

Each species heading is followed by a list of references pertaining to the species. No attempt was made to include complete synonymies but the references indicate the various names proposed for each species and may include important taxonomic studies, faunal works, catalogue listings and biological studies.

The North American range of species is outlined in very general terms from published distributional records. Saskatchewan locality records for each species are listed and are plotted on a map.

Measurements are presented at the beginning of species descriptions; length is measured from the most anterior portion of the head to the tip of the folded wings and for brachypterous specimens is from the anterior margin of the head to the end of the abdomen.

The species description is a diagnostic statement presenting the principal characters which separate males, females, and nymphs of the species from related forms, even though the related types may not occur in Saskatchewan.

Illustrations augment keys and descriptions. Drawings of male and female genitalia are given for nearly every species. For species where representatives were not collected in this study, and were not borrowed from W.E. Ricker for examination, drawings are not presented.

Table 1. Systematic List of the Stoneflies of Saskatchewan.

ORDER PLECOPTERA

Family Pteronarcidae

Genus *Pteronarcys* Newman 1838*Pteronarcys dorsata* (Say) 1823Genus *Pteronacella* Banks 1900*Pteronacella badia* (Hagen) 1873

Family Taeniopterygidae

Genus *Taeniopteryx* Pictet 1841*Taeniopteryx nivalis* (Fitch) 1847Genus *Oemopteryx* Klapálek 1902*Oemopteryx foscetti* (Ricker) 1965

Family Capniidae

Genus *Capnia* Pictet 1841*Capnia confusa* Claassen 1936*Capnia coloradensis* Claassen 1937*Capnia gracilaria* Claassen 1924*Capnia vernalis* Newport 1848Genus *Utacapnia* Nebeker and Gaufin 1971*Utacapnia trava* (Nebeker and Gaufin) 1965Genus *Isocapnia* Banks 1938*Isocapnia crinita* (Needham and Claassen) 1925*Isocapnia missourii* Ricker 1959Genus *Paracapnia* Hanson 1946*Paracapnia angulata* Hanson

Family Nemouridae

Genus *Nemoura* Latreille 1976*Nemoura rickeri* Jewett 1971Genus *Podmosta* Ricker 1952*Podmosta delicatula* (Claassen) 1923Genus *Zapada* Ricker 1952*Zapada cinctipes* (Banks) 1897Genus *Amphinemura* Ris 1902*Amphinemura linda* (Ricker) 1952Genus *Shipsa* Ricker 1952*Shipsa rotunda* (Claassen) 1923Genus *Malenka* Ricker 1952*Malenka californica* (Claassen) 1923

Family Leuctridae

Genus *Leuctra* Stephens 1835

Leuctra ferruginea (Walker) 1852

Genus *Paraleuctra* Hanson 1941

Paraleuctra vershina Gaufin and Ricker 1975

Family Chloropterlidae

Genus *Hastaperla* Ricker 1935

Hastaperla brevis (Banks) 1895

Genus *Suwallia* Ricker 1943

Suwallia lineosa (Banks) 1918

Genus *Triznaka* Ricker 1952

Triznaka signata (Banks) 1895

Family Perlidae

Genus *Paragnetina* Klapalek 1907

Paragnetina media (Walker) 1852

Genus *Claassenia* Wu 1934

Claassenia sabulosa (Banks) 1900

Genus *Acroneuria* Pictet 1841

Acroneuria lycorias (Newman) 1839

Acroneuria abnormis (Newman) 1838

Genus *Hesperoperla* Banks 1938

Hesperoperla pacifica (Banks) 1900

Genus *Perlesta* Banks 1906

Perlesta placida (Hagen) 1861

Family Perlodidae

Genus *Arcynopteryx* Klapalek 1904

Arcynopteryx compacta (MacLachlan) 1872

Genus *Skwala* Ricker 1943

Skwala parallela (Frison) 1936

Genus *Diura* Billberg 1820

Diura bicaudata (Linnaeus) 1758

Genus *Isogenoides* Klapalek 1758

Isogenoides colubrinus (Hagen) 1874

Isogenoides frontalis (Newman) 1838

Genus *Isoperla* Banks 1906

Isoperla bilineata (Say) 1823

Isoperla decolorata (Walker) 1852

Isoperla longiseta Banks 1906

Isoperla marlynia Needham and Claassen 1925

Isoperla patricia Frison 1942

Isoperla petersoni Needham and Christensen 1927

Isoperla transmarina (Newman) 1838

SYSTEMATICS

The following keys to families and genera apply only to stoneflies known from Saskatchewan, and are modified from Needham and Claassen (1925), Harper and Hynes (1971b, 1971d), Gaufin *et al.* (1972) and Hitchcock (1974). Keys for nymphs will not separate the very early instars.

Key to families and genera of adult Plecoptera known from Saskatchewan

1	Paraglossae and glossae subequal in length (Fig. 21)	2
1'	Paraglossae much longer than glossae (Fig. 20)	23
2 (1)	Remnants of branched gills on abdominal segments 1 and 2 (Fig. 6, 7); anal area of forewing with two or more rows of crossveins.....	
 <i>Pteronarcidae</i>	3
2'	No gill remnants on abdominal segments 1 and 2; anal area of forewing without crossveins or with only one row of them (Fig. 33, 34, 36, 37, 39)	4
3 (2)	Gill remnants on abdominal segment 3 (Fig. 7)	<i>Pteronarcella</i> , p. 21
3'	Gill remnants absent from abdominal segment 3 (Fig. 6)	<i>Pteronarcys</i> , p. 19
4 (2')	Tarsal article 2 much shorter than article 1 in lateral view (Fig. 23)	6
4'	Article 2 at least as long as article 1 in lateral view (Fig. 22)	
 <i>Taeniopterygidae</i>	5
5 (4')	Each coxa with small, round membranous areas on its ventral surface; male cercus with one article (Fig. 40, 43); female sternum 9 without long projection extended across sternum 10 (Fig. 44)	<i>Taeniopteryx</i> , p. 22
5'	Coxae without membranous areas on ventral surfaces; male cercus with at least 3 articles (Fig. 42); female sternum 9 with long projection extended across sternum 10 (Fig. 45)	<i>Oemopteryx</i> , p. 23
6 (4)	Cercus of more than one article (Fig. 50-72); A ₂ of forewing unbranched (Fig. 37)	
 <i>Capniidae</i>	20
6'	Cercus of only one article (Fig. 73-92); A ₂ of forewing branched (Fig. 34, 36)	7
7 (6')	Wings flat at rest; last article of labial palpus in ventral view subcircular, larger than subterminal article (Fig. 29)	<i>Nemouridae</i> 9
7'	Wings rolled around body at rest; last article of labial palpus in ventral view longer than wide, equal in length to subterminal article (Fig. 21)	
 <i>Leuctridae</i>	8
8 (7')	m-cu of hindwing connected to Cu ₁ before it divides (Fig. 36); male cercus normal, without point or projections (Fig. 84)	<i>Leuctra</i> , p. 41
8'	m-cu crossvein of hindwing connected to Cu ₁ after it divides (Fig. 34); male cercus with sharp projections or pointed (Fig. 81, 83)	<i>Paraleuctra</i> , p. 42
9 (7)	Males: Supra-anal process present (Fig. 73-77, 79); flaplike ventral lobe arising from base of 8th abdominal sternum (Fig. 78, 80)	15
9'	Females: no supra-anal process; no ventral lobe; 8th abdominal sternum modified as subgenital plate (Fig. 85-90)	10
10 (9')	Gill remnants under neck or head (Fig. 10)	11
10'	Gill remnants absent	13
11 (10)	Gills of most specimens of five branches	<i>Zapada</i> , p. 36
11'	Gills with six or more branches	12

12	(11')	7th abdominal sternum with large, sclerotized posterior projection which extends onto 8th sternum (Fig. 88)	<i>Amphinemura</i> , p.	37
12'		7th abdominal sternum with small pointed posterior projection not extended onto 8th sternum (Fig. 85)	<i>Malenka</i> , p.	39
13	(10')	Sternum 7 sclerotized, produced over full length of 8, its hind margin straight to broadly rounded (Fig. 89)	<i>Nemoura</i> , p.	34
13'		Sternum 7 only slightly or not at all produced over 8; though the narrowly rounded margin of the subgenital plate of the sternum 8 in <i>Shipsa</i> may be mistaken for sternum 7		14
14	(13')	Sternum 8 with subgenital plate terminated anterior to its well-developed hind margin (Fig. 87)	<i>Shipsa</i> , p.	38
14'		Sternum 8 with narrow median sclerotized band contrasted sharply with unsclerotized field at either side (Fig. 90)	<i>Podmosta</i> , p.	35
15	(9)	Gills present, cervical (Fig. 10)		16
15'		Gills absent		18
16	(15)	Gills of most specimens with five branches	<i>Zapada</i> , p.	36
16'		Gills with six or more branches		17
17	(16')	Cerci with mesobasal lobe (Fig. 73)	<i>Malenka</i> , p.	39
17'		Cerci without mesobasal lobe (Fig. 77)	<i>Amphinemura</i> , p.	37
18	(15')	Cerci elongate, heavily sclerotized distally, inner surface membranous, tip sharp or with two or more processes (Fig. 79, 80)	<i>Nemoura</i> , p.	34
18'		Cerci membranous or weakly sclerotized, tip blunt, without spines or processes (Fig. 75, 76)		19
19	(18')	Sides of 10th tergum produced into erect in-curved spiny processes (Fig. 75) ..	<i>Shipsa</i> , p.	38
19'		Sides of 10th tergum not as above (Fig. 76)	<i>Podmosta</i> , p.	35
20	(6)	Male supra-anal process simple, comprised of one element; female subgenital plate without notch or conspicuous pattern		21
20'		Male supra-anal process of two distinct elements, one dorsal one ventral (Fig. 50, 51); female subgenital plate slightly notched, sternum 8 with conspicuous pattern (Fig. 69) ..	<i>Utacapnia</i> , p.	31
21	(20)	R ₁ of forewing strongly bent upward at origin, A ₁ bent abruptly caudad at junction of cu-a, then curved laterad (Fig. 37)	<i>Capnia</i> , p.	26
21'		R ₁ and/or A ₁ of forewing straight (Fig. 33, 39)		22
22	(21')	Prothoracic and mesothoracic presterna broadly united with basisterna (Fig. 18); forewing R ₁ straight at origin (Fig. 39); male with lobe on 9th sternum (Fig. 62)	<i>Isocapnia</i> , p.	32
22'		Prothoracic and mesothoracic presterna separated from basisterna (Fig. 19); R ₁ of forewing slightly curved upward at origin (Fig. 33); male 9th sternum without lobe	<i>Paracapnia</i> , p.	25
23	(1')	remains of branched gills at lower angles of thorax; cu-a of forewing in most specimens either in anal cell or distant from it by no more than its own length		24
23'		Remains of branched gills absent from thorax; cu-a, if present, generally distant from anal cell by more than its own length (Fig. 32, 35, 38)		28
24	(23)	Males with raised knob or "hammer" on 9th sternum (Fig. 9); female subgenital plate without deep notch (Fig. 99, 100, 104, 106)		26
24'		Males without "hammer" on 9th sternum, female subgenital plate deeply notched		25

25	(24')	Distinct Y-shaped mesosternal ridge pattern (Fig. 24, 25) hind margin of male 10th tergum deeply cleft, with dorsal projections (genital hooks) extended forward from sides of the cleft; female subgenital plate not hairy (Fig. 105).....	<i>Paragnetina</i> , p.	46
25'		Mesosternal ridge pattern not in distinct, dark Y-shape; hind margin of male 10th tergum not cleft, no dorsal projections on 10th tergum, paraprocts joined; female subgenital plate covered with long hairs.....	<i>Perlesta</i> , p.	52
26	(24)	Male tergum 10 with hooks arising from lateral angles; paraprocts normal (Fig. 8)	<i>Claassenia</i> , p.	48
26'		Male tergum 10 unmodified; paraprocts formed as recurved hooks (Fig. 101-103).....		27
27	(26)	Subanal lobes of male very broadly triangular, terga 9, 10 not covered with spinules (Fig. 101); female subgenital plate considerably produced (Fig. 104) ...	<i>Hesperoperla</i> , p.	51
27'		Subanal lobes of male slender hooks, terga 9 and 10 with many spinules (Fig. 102, 103); female subgenital plate little if any produced (Fig. 99, 100).....	<i>Acroneuria</i> , p.	49
28	(23')	A ₂ of forewing either not forked or forked beyond anal cell (i.e., two main anal veins, and 2nd of which is forked in some species) (Fig. 32).....		
	Chloroperlidae		29
28'		Fork of A ₂ of forewing included in anal cell, so that two branches leave cell separately (i.e., there are three main anal veins) (Fig. 35, 38)	Perlodidae	31
29	(28)	Anal area of hindwing apparently absent (Fig. 32)	<i>Hastaperla</i> , p.	43
29'		Anal area of hindwing present		30
30	(29')	Head unmarked except for ocellar rings (Fig. 163); males with finger-like process directed inward from basal article of each cercus (Fig. 95); female subgenital plate emarginate (Fig. 98).....	<i>Suwallia</i> , p.	44
30'		Head with conspicuous markings of black on yellow, ocellar triangle dark with anterior mark on head as long as broad (Fig. 164); no process at base of male cerci (Fig. 94); female subgenital plate broadly rounded (Fig. 97)	<i>Triznaka</i> , p.	45
31	(28')	Males: paraprocts modified as recurved hooks, or considerably produced posterad, or genitalia complicated by various stylets and sclerotized areas		32
31'		Females: paraprocts unmodified; genitalia simple, 8th sternite generally produced as genital plate.....		36
32	(31)	10th tergum completely cleft; genitalia complicated by stylets or various unsclerotized structures (Fig. 110, 111)	Isogeninae	33
32'		10th tergum entire, at most slightly notched; genitalia simple (Fig. 107).....		35
33	(32)	Wings with four-to-many crossveins beyond cord, generally arranged in irregular network (Fig. 35); 7th sternum without lobe.....		34
33'		Wings with no more than two crossveins beyond cord (Fig. 38); 7th sternum generally with lobe	<i>Isogenoides</i> , p.	55
34	(33)	Supra-anal process very long, needle-like; lateral stylets absent (Fig. 113)		
	 <i>Arcynopteryx</i> , p.		53
34'		Supra-anal process blunt, not unusually long; lateral stylets present (Fig. 112)		
	 <i>Skwala</i> , p.		54
35	(32')	Paraprocts produced postero-mesad, meeting along their inner faces (Fig. 107); no lobe on 8th sternum	Perlodinae.....	
	 <i>Diura</i> , p.		55
35'		Paraprocts forked as hooks or only slightly modified (Fig. 117-123); 8th sternum always with a lobe.....		
	Isoperlinae	<i>Isoperla</i> , p.	57

36	(31')	Numerous irregular crossveins between Rs and R (Fig. 35)	37
36'		Apical crossveins few or absent.....	38
37	(36)	Subgenital plate generally produced more than halfway across ninth sternum; caudal margin slightly emarginate (Fig. 115)	<i>Arcynopteryx</i> , p. 53
37'		Subgenital plate generally produced less than halfway across ninth sternum; caudal margin straight (Fig. 114)	<i>Skwala</i> , p. 54
38	(36')	Submental gills present (Fig. 20)	<i>Isogenoides</i> , p. 55
38'		Submental gills absent	39
39	(38')	General color dark brown with yellow median stripe on pronotum; hairs on margin of groove in femur of proleg not noticeably longer than other hairs on femur; subgenital plate produced halfway or more across 9th sternum (Fig. 108, 109)	<i>Diura</i> , p. 55
39'		Not as above.....	<i>Isoperla</i> , p. 57

Key to families and genera of Plecoptera nymphs known from Saskatchewan

1		Glossae and paraglossae subequal in length (Fig. 21).....	2
1'		Paraglossae extended greatly beyond glossae (Fig. 20)	16
2	(1)	Branched gill tufts on abdominal segments 1 and 2 (Fig. 6, 7).....	
	Pteronarcidae.....	3
2'		Branched gill tufts absent from abdominal segments 1 and 2	4
2	(2)	Gill tufts on first two abdominal segments (Fig. 6)	<i>Pteronacys</i> , p. 19
3'		Gill tufts on first three abdominal segments (Fig. 7)	<i>Pteronarcella</i> , p. 21
4	(2')	Tarsi in lateral view with 2nd article much shorter than 1st (Fig. 23).....	6
4'		Tarsi in lateral view with 2nd article at least as long as 1st (Fig. 22).....	5
5	(4')	A single retractile gill on each coxa (Fig. 13)	<i>Taeniopteryx</i> , p. 22
5'		No coxal gills.....	<i>Oemopteryx</i> , p. 23
6	(4)	Extended hind legs exceed end of abdomen; hindwing pads divergent from axis of body (Fig. 14); cervical gills present in some species (Fig. 11, 12)	
	Nemouridae	7
6'		Extended hind legs not exceeding end of abdomen; hindwing pads subparallel to axis of body (Fig. 15); gills absent	11
7	(6)	Species with four prosternal gills (Fig. 11, 12)	8
7'		Species without gills	9
8	(7)	Prosternal gills commonly five-branched (Fig. 11)	<i>Zapada</i> , p. 36
8'		Prosternal gills with six or more branches (Fig. 12)	
	 <i>Malenka</i> , p. 39, <i>Amphinemura</i> , p. 37	37
9	(7')	Pronotum with well-defined lateral fringe of hairs (Fig. 146)	<i>Nemoura</i> , p. 34
9'		Pronotum without definite fringe of hairs; bristles on lateral margins of pronotum may sometimes be longer than dorsal bristles, but are never set in a distinct line.....	10
10	(9')	Femora with continuous fringe on long silky hairs; legs banded	<i>Shipsa</i> , p. 38
10'		Femora without fringe; legs not banded	<i>Podmosta</i> , p. 35
11	(6')	First eight abdominal segments divided to tergum and sternum by membranous fold (Fig. 138-140).....	<i>Capniidae</i>
			13
11'		First six or less abdominal segments divided to tergum and sternum by membranous fold (Fig. 27).....	<i>Leuctridae</i>
			12
12	(11')	First four abdominal segments divided laterally (Fig. 27); labial palpi extended well beyond paraglossae (Fig. 21).....	<i>Leuctra</i> , p. 41

12'	First six abdominal segments divided laterally; labial palpi extended approximately to tip of paraglossae.....	<i>Paraleuctra</i> , p.	42
13 (11)	Long swimming hairs along cerci (Fig. 26)	<i>Isocapnia</i> , p.	32
13'	Cerci without long swimming hairs		14
14 (13')	Body with numerous conspicuous bristles; head capsule with reticulate purplish pattern .	<i>Paracapnia</i> , p.	25
14'	Bristles inconspicuous; head capsule without elaborate pattern		15
15 (14')	Erect bristles on posterior margin of abdominal terga very long, nearly as long as mid-dorsal length of segment	<i>Utacapnia</i> , p.	31
15'	Erect bristles shorter, half (or less) mid-dorsal length of tergum (Fig. 138-140)	<i>Capnia</i> , p.	26
16 (1')	Tufts of filamentous gills on thorax.....	Perlidae.....	17
16'	Thoracic gills absent		21
17 (16)	Spinules or long hairs set in row across back of head forming occipital ridge (Fig. 4, 5) .		18
17'	No spinules in row across back of head except near hind margin of eye (i.e., no occipital ridge)(Fig. 2)		20
18 (17)	Subanal gills absent (Fig. 5)	<i>Paragnetina</i> , p.	46
18'	Subanal gills present (Fig. 4)		19
19 (18')	Abdomen with numerous "freckles"	<i>Perlesta</i> , p.	52
19'	Abdomen without numerous "freckles", but uniformly brown above (Fig. 4)	<i>Claassenia</i> , p.	48
20 (17')	Head with central light spot anterad of median ocellus (Fig. 3)	<i>Hesperperla</i> , p.	51
20'	Head without central light spot; with a light M-pattern in front of anterior ocellus (Fig. 1, 2)	<i>Acroneuria</i> , p.	49
21 (16')	Hindwing pads at angle to axis of body (Fig. 168); cerci as long as, or longer than, abdomen; body commonly patterned; particles of maxillary palpus evenly tapered from 1st to 5th (Fig. 170)	Perlodidae	24
21'	Hindwing pads subparallel to axis of body (Fig. 159); cerci three-quarters length of abdomen; body usually uniformly brown; last article of maxillary palpus abruptly thinner than previous articles (Fig. 162)	Chloroperlidae	22
22 (21')	Inner margin of hindwing pads straight; body of mature nymph 7 mm or less	<i>Hastaperla</i> , p.	43
22'	Inner margin of hindwing pads sinuate or notched (Fig. 159); body of mature nymph larger than 7 mm		23
23 (22')	Abdominal terga each with two light colored spots laterally, and central median stripe (Fig. 159)	<i>Triznaka</i> , p.	45
23'	Abdomen uniformly brown above	<i>Suwallia</i> , p.	44
24 (21)	Arms of mesosternal Y-ridge approach or meet anterior corners of furcal pits (Fig. 25) .		25
24'	Arms of mesosternal Y-ridge meet posterior corners of furcal pits (Fig. 24)		26
25 (24)	Denticles numerous along both sides of outer cusps of both mandibles (Fig. 28)	<i>Skwala</i> , p.	54
25'	Denticles absent from cusps of nymphal mandible, or a few present on outer left cusp only	<i>Arcynopteryx</i> , p.	53
26 (24)	Single fingerlike gills at each basal corner of submentum (Fig. 20)	<i>Isogenoides</i> , p.	55
26'	Submental gills absent		27
27 (26')	Abdominal terga dark, with two dorsolateral spots and a few small lateral spots;		

- 27' lacinia of maxilla with sharp angle below small tooth (Fig. 30).....*Diura*, p. 55
 Abdominal terga with longitudinal or transverse markings or dark dots (Fig. 168);
 lacinia without sharp angle low small tooth, rounded or, more commonly, tapered
 from tooth to base (Fig. 170).....*Isoperla*, p. 57

Family Pteronacidae

Pteronacids are large, primitive stoneflies occurring in North America and eastern Asia. They are characterized by many-articled cerci, long antennae and wings with numerous cross-veins. The adult male has no vesicle on the ninth sternum and has a conspicuous epiproct and paraprocts on the cleft 10th tergum. Nymphs have gill tufts on the thorax and first two abdominal segments. There are two North American genera in this family; both occur in Saskatchewan.

Genus *Pteronarcys* Newman

Ricker (1925) proposed two subgenera of *Pteronarcys*, *Allonarcys* and *Pteronarcys sensu strictu*, which were later ranked as genera by Illies (1966). *Allonarcys* occurs in eastern North America and adults are characterized by an upright epiproct, cupped paraprocts, the ninth sternum unnotched and without peglike setae at the tip, divided hemitergal lobes on the male tenth tergum and produced female subgenital plates. Nymphs have paired lateral projections on abdominal segments. *Pteronarcys* adults differ by having massive epiprocts, fleshy, rounded paraprocts, the ninth sternite notched and with peglike setae near the tip, hemitergal lobes on the tenth tergite projected posterad (Fig. 46), and unproduced female subgenital plates (Fig. 47, 48). Nymphs lack paired lateral projections of the abdominal segments. Six species of *Pteronarcys* are known in North America and the range of one species extends into Saskatchewan.

Pteronarcys dorsata Say (Fig. 6, 46-48, 180)

Sialis dorsata (Say) 1823: 164.

Pteronarcys dorsata, Frison 1942a: 242. – Harden and Mickel 1952: 9. – Ricker 1964: 68. – Hitchcock 1974: 234. – Baumann, Gaufin, and Surdick 1977: 116.

Pteronarcys dorsata, the one species of this genus found in Saskatchewan, has a transcontinental distribution which extends from Laborador to Alaska, south in the Rockies to Wyoming and in the east to the Great Lakes and south to Georgia. Previous Saskatchewan records include Cushing's (1961) report from Montreal River, Ricker's (1944) record from Wapusk River in the Reindeer Lake region, a record from Saskatchewan River (Smith, 1917) and a report from the South Saskatchewan River at Saskatoon (Ricker, 1946). New Saskatchewan records (Fig. 180) include: North Saskatchewan River at Jct. Hwy. 5 (Borden Bridge) and at the ferry 10 mi. E. of Prince Albert, Sask.; South Saskatchewan River at ferry N of Birch Hills, Sask. and at the ferry N. of Lemsford, Sask.; Nipekamew River, Jct. Hwy. 165; Weyakwin River, Jct. Hwy. 2; Waskesiu River, Jct. Hwy. 2; Torch River, Jct. Hwy. 106; Arsenault River, Jct. Hwy. 104; Nemeiben River, Jct. Hwy. 2; Puskwakau River, Jct. Hwy. 2; Puskwakau River, Jct. Hwy. 106; river at mile 34, Jct. Hwy. 105; creek at mile 120, Jct. Hwy. 105; stream 85 mi. N. of La Ronge, Sask., Jct. Hwy. 102; Battle River, 4 mi. S. of Lashburn, Sask.; Overflowing River, Jct. Hwy. 109; Jackfish Creek, Jct. Hwy. 8; Meeyomoot River, Jct. Hwy. 165;

McDougal Creek, Jct. Hwy. 120; Bear River, Jct. Hwy. 106; Martineau River, Jct. Hwy. 55; Mackay Creek, Jct. Hwy. 2; Mackenzie Creek, near Hwy. 165; Bow River, Jct. Hwy. 165, Swan River, Jct. Hwy. 8; Ballantyne River, Jct. Hwy. 106; Churchill River, Jct. Hwy. 2, Wintego Lake Rapids, and Iskwatam lake; Fond du Lac River at outflow of Black Lake; stream at mile 30, Wollaston Lake Road; Caribou Creek, Jct. Hwy. 106; Red Deer River, 2 mi. S. of Hudson Bay, Sask.; and Torch River, Jct. Hwy. 106.

Ricker (1964) presented a North American distribution map for the species.

Diagnostic Characters. – Average length of males, 40.0 mm; females, 60.0 mm (from anterior margin of head to tip of folded wings). Male genitalia with ninth sternum straight near tip; epiproct large, flattened, complex in shape (Fig. 46). Female subgenital plate straight, or with two small projections (Fig. 47, 48).

Nymphal females with projection on tenth tergum projected postero-dorsad to point; nymphal males with projection extended postero-ventrad with peg on caudal surface. Mature male nymphs with a nearly rectangular projection posterad on ninth abdominal sternum.

Needham and Claassen (1925), Nelson and Hanson (1971) and Hitchcock (1974) figured the adult genitalia, and Claassen (1931) figured the nymph.

Bionomics. – Nymphs of this species are common in streams and large rivers. Nymphs occur in rapids (Smith, 1917) and in trash from eddies below stony rapids (Gauvin *et al.*, 1972).

Hilsenhoff and Narf (1972) stated that the life cycle of *Pteronarcys dorsata* is at least two years in Wisconsin; the aquatic stage of *Pteronarcys californica* Newport lasts three years (Elder and Gauvin, 1973). In Saskatchewan, three size classes of *Pteronarcys dorsata* nymphs have been collected at one time, suggesting a three year life cycle. Eight mature nymphs with fully developed wing pads collected at Weyakwin River on June 9, 1975 averaged 34.2 mm long; seven immature nymphs with no wing pad development averaged 17.0 mm long and ten very immature nymphs averaged 12.3 mm in length. Eggs appear to hatch directly and nymphs are likely the overwintering stage since ten nymphs averaging 5.1 mm long were collected at the same river on July 16, 1975, about two months after adult emergence. In Saskatchewan, adult emergence occurs in early June and lasts approximately three weeks.

Pteronarcys dorsata nymphs are detritivores, eating leaves and other vegetable matter that falls into the water. They can be maintained in an aquarium on a diet of dead leaves which are skeletonized (Harden and Mickel, 1952).

Nebeker (1971a) found the longevity of adults was related inversely to the temperature at which the nymphs were maintained. At 10 C the mean life span was 36 days; it was 31 days at 15 C and 17.5 days at 20 C. It was also found that the stonefly could live at higher temperatures than levels where good development and successful emergence occurs. Highest feeding rates were observed at 20 C (no feeding occurred at 1 C and 35 C); the best temperature for emergence was 15 C. Females reared at 15 C produced, on average, 475 eggs, but at 20 C only one female oviposited and then laid only 175 eggs. Water temperature had a great influence on development: at 5 C nymphs did not develop for a nine month testing period (Nebeker, 1971a), but at a constant 20 C adults emerged five months earlier than they normally do in the field, and the separate emergence of the sexes was far more pronounced than is normal (Nebeker, 1971b).

Cushing (1961) reported collecting *Pteronarcys dorsata* in rapids of Montreal River above four associated lakes, but not in rapids below the lakes. A possible explanation for this absence was proposed by Lehmkuhl (1972), who pointed out that one major effect of a large reservoir is to alter the thermal regime of an outflowing river, making it possible for some aquatic insects to complete their life cycles in the river near the reservoir.

Genus *Pteronarcella* Banks

Adults of *Pteronarcella* resemble those of *Pteronarcys* but are only about half the size. Crossveins are fewer, and they are entirely absent from radial areas of the wing. The male ninth abdominal segment is elevated in a broad, transversely recurved scoop-like lobe. Some of the segments above this lobe bear paired dorsal humps at the sides. At rest, the large U-shaped supra-anal process is concealed between the subanals and the divided halves of the tenth segment. Female subgenital plates are not produced over the ninth sternite (Fig. 44). Nymphs have gills on the first three abdominal segments, with the tenth segment produced into a triangular, pointed, conical process. Two species are known in North America; one is found in Saskatchewan.

Pteronarcella badia (Hagen)
(Fig. 49, 180)

Pteronarcys badia Hagen 1874: 573.

Pteronarcella triloba, Smith 1917: 461, 462.

Pteronarcella badia, Claassen 1940: 23. – Jewett 1956: 57. – Ricker 1964: 55. – Baumann, Gaufin and Surdick 1977: 112.

Pteronarcella badia, the only species of *Pteronarcella* in Saskatchewan, is common in the Rocky Mountain region and extends eastward in Montana, Utah and Arizona. New Saskatchewan records, (Fig. 180) include: Broad Creek, Jct. Hwy. 104 and Mistohay Creek, Jct. Hwy. 226.

Diagnostic Characters. – Average length, males 15.0 mm (from anterior portion of head to tips of folded wings); females, 20.0 mm. Male genitalia with appendage on ninth dorsal abdominal segment broadly rounded at apex, side margins sinuous. Hind margin of female subgenital plate rounded, truncate and slightly trilobate but not acutely notched (Fig. 49).

Nymphal gill filaments at least twice as long as basal conical process of gill tufts.

Needham and Claassen (1925), Jewett (1956), Gaufin *et al.* (1966) and Gaufin *et al.* (1972) figured the adult genitalia, and Claassen (1931) figured the nymph.

Bionomics. – Richardson and Gaufin (1971) report that nymphs generally occur in slow areas of streams in Utah and Colorado where debris collects. However, in Saskatchewan, nymphs were commonly collected from swiftly flowing areas of the streams.

Gaufin *et al.* (1972) state that the life cycle probably lasts two years. In Saskatchewan, adult emergence was during the first week of June in 1975. It appears that the eggs hatch in a short period since 11 nymphs averaging 3.9 mm long were collected in mid-July. The nymphs would be the overwintering stage.

Nymphs of *Pteronarcella badia* are predominantly herbivorous though some individuals feed on animal material when plant matter is unavailable or scarce. (Richardson and Gaufin, 1971).

Family Taeniopterygidae

Taeniopterygids have tarsal articles subequal in length; epiprocts of males are prominent and paraprocts are generally greatly modified. Adults are also characterized by cu-m intercubital crossveins. The range includes North America, Eurasia, and northern Africa.

Zwick (1973) recognized two subfamilies. Taeniopteryginae includes the single genus *Taeniopteryx*, and 13 genera are recognized in the Brachypterinae. Ricker and Ross (1975) discussed the distinguishing characters of the two subfamilies. In Brachypterinae, the male ninth sternite is scoop-like

and greatly produced beyond the tenth segment. Inner members of male subanal lobes are complex, asymmetrical and partly membranous. Male cerci have at least two articles. The female ninth sternite is produced well beyond the base of the subanal lobes and coxal gills are absent.

In Taeniopteryginae the male ninth sternite is not scoop-shaped and extends very little beyond the tenth segment. Males have simple, symmetrical and sclerotized subanal lobes, and lack a basicercal process. The female subgenital plate is somewhat produced over the tenth segment and rounded but does not extend to the subanal lobes. Male cerci have a single article and coxal gills are present. Both subfamilies of Taeniopterygidae are represented in Saskatchewan by *Taeniopteryx nivalis* of the Taeniopteryginae, and *Oemopteryx fosketti* of the Brachypterinae.

Genus *Taeniopteryx* Pictet

Nymphs of this genus have coxal gills (Fig. 13). Adults have membranous circular areas on each coxa, which represent coxal gill scars. Male paraprocts are concealed within the ninth sternite and there are usually two membranous lobes behind the female subgenital plate (Fig. 44). Eight *Taeniopteryx* species are known in North America; one species occurs in Saskatchewan.

Taeniopteryx nivalis (Fitch) (Fig. 13, 40, 41, 43, 44, 181)

Nemoura nivalis Fitch 1847: 274.

Taeniopteryx nivalis, (in part) Needham and Claassen 1925: 240. – Harden and Mickel 1952: 12. – Ricker and Ross 1968: 1434.

Taeniopteryx maura, (in part) Frison 1942a: 248. – Jewett 1959: 55, and 1960: 151.

Taeniopteryx nivalis ranges from Laborador through Quebec and Ontario to Minnesota and south to Pennsylvania, northern Indiana and Illinois. Western records include Oregon and Alberta with this as the first Saskatchewan record. The Saskatchewan distribution (Fig. 181) includes the following localities: Waskesiu River, Jct. Hwy. 2; Crean River, Jct. Hwy. 2; Weyakwin River, Jct. Hwy. 2; Montreal River, Jct. Hwy. 2 (mile 65); Little Red River near Prince Albert, Sask.; Jackfish Creek, Jct. Hwy. 8; Torch River, Jct. Hwy. 106; McDougal Creek, Jct. Hwy. 120, Nipekamew River, Jct. Hwy. 165; and Caribou Creek, Jct. Hwy. 120.

Diagnostic Characters. – Average length males, 11.0 mm (from anterior margin of head to tip of folded wings); females, 17.0 mm. Males without spurs or other projections on hind femur; with vesicle or ventral lobe on ninth sternite, 2–3 times long as wide. Hairs on hind margin of the ninth sternite directed downward, and forward generally much shorter than those situated more anteriorly on sternite (Fig. 40). Aedeagus without brown sclerotized band between the two lateral lobes (Fig. 41). Females with strongly sclerotized V-shaped notch on eighth sternite, produced sides of the notch in contact at acute angle (Fig. 44).

Abdomen of nymph with mid-dorsal stripe or several light dots on the posterior margin of each segment. Abdominal tergites with short, thick bristles and a few long hairs on hind margins.

Needham and Claassen (1925) figured the female; Claassen (1931) and Harper and Hynes (1971c) illustrated the nymphs. Figures of the male genitalia are presented in Fig. 40, 41, and 43.

Bionomics. – Harper and Hynes (1970) determined that the life cycle of *Taeniopteryx nivalis* is univoltine; eggs are deposited in April and May, hatch directly, and nymphs diapause in an undetermined instar (4 or 5). In diapausing nymphs, fat globules accumulate, all bristles are lost, cerci are cast off, legs are folded and head and antennae are reflexed under the thorax. Diapausing nymphs

have not been found in streams probably because they burrow deep into the substratum. Summer diapause enables early instar nymphs to survive high water temperatures; later instars are extremely heat sensitive (Nebeker and Lemke, 1968). Diapause ends in late September (Harper and Hynes, 1972) and most growth occurs in winter (Harper and Hynes, 1970).

Coleman and Hynes (1970) and Harper and Hynes (1972) reported rapid growth from October through the winter months. Emergence of adults begins in mid-March and lasts about one week. Mating occurred soon after emergence. Harper and Hynes (1972) noted that oviposition began about one week after the maximum period of emergence and adults lived for about one month in the field. Under simulated stream conditions in the laboratory, egg hatching occurred about 40 days after oviposition.

In Saskatchewan, adults emerged during the end of March of 1976. Adults remained in ice cavities under bridges in early May when all other ice had melted. If removed, adults immediately crawled back to the same cavity or entered another cavity.

Harper and Hynes (1972) found that the species was primarily detritivorous, but occasionally ingested animal matter.

Genus *Oemopteryx* Klapálek

Wings of adult *Oemopteryx* lack costal crossveins and R_s and Cu_1 each have two branches. Males have two epiproct prongs which are usually set together. Outer members of the paraprocts are elongated and heavily sclerotized (Fig. 42). Female subgenital plates are variable, and nymphal characters have been little studied.

Ricker and Ross (1975) noted that there are four well-marked species groups of *Oemopteryx*, the *loewii* group from central Europe, the *contorta* group from the Appalachian Mountains, the *vanduzeeae* group from California and the *glacialis* group from northeastern North America and the plains region. The one species of *Oemopteryx* known from Saskatchewan belongs to the *glacialis* group.

Oemopteryx fosketti (Ricker)

(Fig. 42, 45, 154-158, 171-176, 181)

Brachyptera fosketti Ricker 1965: 475.

Brachyptera zelona, Ricker 1965: 477.

Oemopteryx fosketti, Baumann 1973: 95. – Ricker and Ross 1975: 140

Oemopteryx fosketti is known from the North and South Saskatchewan Rivers, and has also been reported from Utah. The type locality is the South Saskatchewan River at Clarksboro, Sask. The Saskatchewan distribution (Fig. 181) includes the following localities: South Saskatchewan River at Lemsford Ferry, Saskatoon, Sask., and Ferry near Clarksboro, Sask.; and the North Saskatchewan River at Hwy. 5 (Borden Bridge).

Diagnostic Characters. – Average length, females, 10.5 mm (from anterior portion of head to tip of folded wings); males average 7.5 mm (from anterior margin of head to end of abdomen). Males brachypterous, with forewings greatly reduced (about 2.5 mm long) and upturned near the tip; hindwings narrowed and of less than normal length. Male genitalia with supra-anal process divided into four parts: basal bulb brown and smoothly rounded with low, dark, flat, conical apex next to groove separating it from anterior erect member; anterior erect member slender and curved forward with low swellings laterally near tip; posterior erect member near anterior erect member but broader and terminated in two hemispherical membranous bulges separated by angular groove; hind surface of

posterior erect member opened to membranous sleeve or posterior portion of epiproct (Fig. 42). Females with distinct subgenital plate, with hind margin anterior to the hind margin of eighth sternite; subgenital plate rounded and shallowly excavated medially (Fig. 45). The previously unknown nymph is described below.

Description. — Total length of mature nymphs: 10.5 mm (males); 12.0 mm (females).

General color dark brown to nearly black, light yellow ventrally. Head uniformly dark with few dark mottlings near antennae; antennae almost as long as body. Antennal scape and pedicel patterned dorsally as in Fig. 155. Mouthparts as in Fig. 156, 157.

Thoracic nota dark brown; mesonotum with two subrectangular patches of sclerotization at its anterolateral corners. Metanotum with anterior subrectangular sclerotized area separated by membranous area from large metathoracic sclerotized block. Wing pads of mature male nymph pointed and small (the adult is brachypterous); female wing pads normal. Legs yellowish brown, darker at joints; fringes of long hairs along femora, tibiae and tarsi.

Each abdominal tergite with anterior half dark brown, and posterior half light brown. Abdominal terga covered with long clothing hairs; the posterior tergal margin beset with very short bristles and few long hairs (Fig. 158). Sterna 1–7 unsclerotized. Cerci longer than body; cercal articles 1–8 with long bristles, about twice as long as the cercal article; the other articles with whorls of very short bristles, about one-fifth the length of the segment.

Until comparative studies are made of closely related species of this genus, distinguishing characters of the nymph of *Oemopteryx foscetti* cannot be specified.

Bionomics. — Adults emerged on April 16, 17, 18, and 19, 1975 and April 1–4, 1976, at the North Saskatchewan River near Hwy. 5 (Borden Bridge). Water temperature was 0.8 C for the 1975 dates and 1.0 C for the 1976 dates.

Males emerge earlier than females. On April 17, 1975, 121 adults were collected from a small section of the river bank; 106 were males and 15 were females. From a random sample of 79 nymphs collected the same day and reared to adults, 59 were females and 20 were males. This indicated that a significant number of females had yet to emerge. By April 19, 1975, males and females were equally abundant in collections along the river bank: of 77 adults, 41 were males and 36 were females. Earlier male emergence is not uncommon in stoneflies and has been documented for many species. Brinck (1949) suggested a definite advantage to this discrepancy between emergence of the sexes: males are fully developed and ready to mate as soon as females emerge.

Time of ice break-up is probably a critical factor in determining onset of adult emergence. On April 16, 1975, a main channel of water had just started to form but no adults had emerged. By April 17 a main water channel had formed (Fig. 176) and adults were abundant. On April 1, 1976, runoff from highway ditches had melted the river ice under Borden Bridge causing a small opening and adults were present only in this small area. When a large water channel had opened the river adults were numerous along the entire river bank.

Mating occurred immediately after emergence for *Oemopteryx foscetti*: in fact, some males attached to emerging females. After the female had completed ecdysis, they mated immediately.

Males are very active and walk about on snow searching out females (Fig. 171). Many females often remain in small cavities or pockets within the snowbanks (Fig. 172). When discovered by a male, mating usually occurs in the cavity. In one instance, a male encountered a mating pair and also attempted to mate with the female. A struggle ensued (Fig. 173) until one male was driven off. The remaining male mated with the female (Fig. 174).

Abdomens of several *Oemopteryx foscetti* were examined to ascertain degree of egg maturation. Abdomens used were taken from a mature female nymph, an emerging nymph in which the wings had

just begun to leave the nymphal wing pads, a newly emerged female, a fully emerged female collected in the field and a fully emerged female reared in the laboratory.

Abdomens were soaked in 100 percent ethanol for two periods of one hour each, benzene for one hour, one-half benzene and one-half paraffin for one hour and finally were embedded in paraffin. Abdomens were sectioned at 8 microns and placed on glass slides. The slides were dried, the paraffin removed with xylene and stained using Harris' Hematoxylin and Eosin. The tissue was then mounted using Permount. All slides were treated alike.

The eggs appeared similar in all slides studied. In a mature females the eggs stained purple, with a resistant outer covering. No difference was found in a mature female nymph – eggs were in the abdominal cavity and appeared to be as mature as those of a fully developed female. In all abdomens, the eggs appeared identical to eggs which had been deposited on the ice.

Mating soon after adult emergence and the occurrence of mature ova in newly-emerged females is probably an adaptation to the type of habitat in which *Oemopteryx fosketti* lives. After ice break-up occurs, excessive runoff from the surrounding terrain often causes flooding in the North Saskatchewan river. Since emergence occurs as soon as the ice begins to break up, ability to mate and lay eggs immediately ensures that the eggs are fertilized and deposited before the adults may be killed by a flood. Males are brachypterous and could not likely escape a high flood.

The life cycle of this species is probably similar to that described for several other winter stoneflies (Harper and Hynes, 1970). Eggs of winter stoneflies hatch within a month and early-instar nymphs are thought to diapause throughout the summer. Diapause was proposed as an adaptation to survival of high water temperatures in summer. Nymphs in a diapause-like state burrowed deep into the substratum, and this probably explains the absence of members of *O. fosketti* from summer benthic samples. When collected in September, nymphs did not seem to have made any significant growth. Most growth and development occurs during winter.

Family Capniidae

Capniids are small, dark stoneflies characterized by many-articled cerci, wings at rest folded flat on the back, the second tarsal article short, and forewings with only one or two median crossveins and one cubital crossvein. The species are arranged in two subfamilies – the Capniinae of North America, Eurasia and northern Africa, and the Notemourinae of Africa, South America, and Australia and with the single genus *Megaleuctra* in northwestern North America. Four genera of Capniinae *Paracapnia*, *Capnia*, *Utacapnia* and *Isocapnia* occur in Saskatchewan, but the Notemourinae are not known in the province.

Genus *Paracapnia* Hanson

Paracapnia members are distinct in having the mesothoracic postfurcasternal plate united with the furcasternum and the spinasternum (Fig. 19); the meso- and metafurcasternum are transverse and almost rectangular. R_1 of the forewing is bent caudally beyond its base and Cu_1 of the hindwing generally has its apical portion missing (Fig. 33). Two species of this genus are known, and one occurs in Saskatchewan.

Paracapnia angulata Hanson
(Fig. 19, 33, 60, 61, 179)

Paracapnia angulata Hanson 1961: 29. – Hitchcock, 1974: 69.

Capnia opis, Frison 1942a: 264.

Paracapnia angulata and *Paracapnia opis* (Newman) are very closely related and have only recently been recognized as distinct. The geographic range of *Paracapnia angulata* cannot be delimited until previously identified specimens have been checked. This is the first Saskatchewan record of the species; specimens have been collected from the Montreal and Nipekamew Rivers (Fig. 179).

Diagnostic Characters. – Average length, females 8.5 mm (from anterior part of head to tip of folded wings); brachypterous males 4.0 mm (from anterior part of head to end of abdomen). Males of *Paracapnia angulata* are distinguishable from those of *Paracapnia opis* only by the male supra-anal process. In lateral view, *Paracapnia angulata* males have both inner and outer margins of the epiproct angled at the base (Fig. 61). The inner margin is acutely angled or may approach a right angle, but it is not evenly curved as in *Paracapnia opis*. In dorsal view, the epiproct of *Paracapnia angulata* is broadened once and then tapers evenly to the tip (Fig. 60), but the epiproct of male *Paracapnia opis* shows two slight enlargements in dorsal view. Females of these two species are indistinguishable; members of both have the posterior margin of the subgenital plate broadly rounded and with a small, mesal light-colored or membranous spot (Fig. 68).

Nymphs of *Paracapnia angulata* have a long intermediate bristle at the ventral base of the middle and distal cercal articles and short bristles on the inner surface of the tibiae about half as long as the width of the tibia. In *Paracapnia opis* intermediate bristles are absent from cercal articles and the tibial bristles are as long as the width of the tibia.

Hanson (1961) and Harper and Hynes (1971b) figured the adult genitalia; figures of the nymph were published by Harper and Hynes (1971b).

Bionomics. – Harper and Hynes (1972) noted that the emergence pattern of *Paracapnia angulata* was relatively short and synchronous, with the main peak lasting only eight days. Oviposition occurred about one week after emergence and the first nymphs were collected about two months after the appearance of ovipositing females. Growth proceeded rapidly through summer and autumn and by mid-November nearly all specimens had reached the penultimate instar. The last instar was reached by December. Unlike other winter stoneflies, members of *Paracapnia angulata* do not undergo summer diapause, but show significant summer growth.

Harper and Hynes (1970) state that this species is restricted to cold spring-fed streams and thus nymphs are not exposed to high summer water temperatures. Diapause, an adaptation to survival of high summer water temperatures, may then be superfluous since individuals are exposed to low summer water temperatures. In Saskatchewan, *Paracapnia angulata* has been collected in Montreal River and Nipekamew River. Neither of these rivers are spring-fed, but both drain lakes. Lake drainage may affect the temperature scale of out-flowing rivers (Lehmkuhl, 1972), resulting in summer water temperatures which are low enough for *Paracapnia angulata* nymphs to withstand.

Genus *Capnia* Pictet

Adults of this genus are characterized by having vein R_1 of the forewing bent upward toward the costal margin at its origin, and A_1 of the forewing bent caudad at its junction with cu-a and then curved outward (Fig. 37). Thoracic spinasterna are fused to the basisterna, and metathoracic postfurcasternal plates and thoracic presterna are free. Nymphs lack a fringe of cercal bristles. In North America, most

Capnia species are known only from the western part of the continent. Fifty-nine species are known in North America, and four occur in Saskatchewan.

Key to Saskatchewan species of *Capnia*

Adults

- | | | |
|--------|---|--|
| 1 | With supra-anal process recurved forward and above ninth and tenth terga (males) | 2 |
| 1' | Supra-anal process absent (females)..... | 5 |
| 2 (1) | Conspicuous hump on tergum 8; supra-anal process with conspicuous downturned lobe at apex (Fig. 58, 59)..... | <i>Capnia coloradensis</i> Claassen p. 27 |
| 2' | No hump on tergum 8; hump on tergum 7 or absent from all terga | 3 |
| 3 (2') | Supra-anal process extended to tergum 7; a low hump on tergum 7 near anterior edge (Fig. 52, 53) | <i>Capnia gracilaria</i> Claassen, p. 29 |
| 3' | Supra-anal process extended at most to middle of tergum 8, no hump on tergum 7..... | 4 |
| 4 (3') | Supra-anal process expanded at the basal 0.66 of length and narrowed near tip (Fig. 56, 57) | <i>Capnia vernalis</i> Newport, p. 30 |
| 4' | Supra-anal process tapered evenly from base to tip (Fig. 54, 55) | <i>Capnia confusa</i> Claassen, p. 28 |
| 5 (1') | Sterna 7 and 8 united by a median sclerotized connection of various widths | 7 |
| 5' | Sterna 7 and 8 not connected, but separated by membranous area..... | 6 |
| 6 (5') | Posterior edge of sternum 7 membranous with narrow median sclerotized projection extended to or overlapping part of sternum 8 (Fig. 70) | <i>Capnia confusa</i> Claassen, p. 28 |
| 6' | Posterior edge of sternum 7 sclerotized, uniform, unmodified, medially; posterior edge of subgenital plate projected posteriorly usually with low median and lateral projections (Fig. 72)..... | <i>Capnia gracilaria</i> Claassen, p. 29 |
| 7 (5) | Conspicuous subcuticular oval object visible in center of subgenital plate; subgenital plate separated from lateral sclerotized patches by narrow membranous area (Fig. 71) .. | <i>Capnia coloradensis</i> Claassen, p. 27 |
| 7' | Subgenital plate without median oval object, subgenital plate united to lateral sclerotized patches (Fig. 67) | <i>Capnia, vernalis</i> Newport, p. 30 |

Nymphs

- | | |
|--------|---|
| 1 | Tip of galea expanded, with fringe of long hairs (Fig. 141).. <i>Capnia vernalis</i> Newport, p. 30 |
| 1' | Tip of galea evenly tapered or pointed (Fig. 142-144)..... 2 |
| 2 (1') | Long setae on head about equal to diameter of eye, male supraanal lobe long (Fig. 138) |
| | <i>Capnia gracilaria</i> Claassen, p. 29 |
| 2' | Long setae on head about equal to half diameter of eye, male supra-anal lobe short (Fig. 139, 140)..... |
| | <i>Capnia confusa</i> Claassen, p. 28; <i>Capnia coloradensis</i> Claassen, p. 27 |

Capnia coloradensis Claassen
(Fig. 58, 59, 71, 140, 144, 177)

Capnia coloradensis Claassen 1937: 79. – Claassen 1940: 92. – Hanson 1946: 238. – Ricker 1965: 487. – Gaufin, Nebeker and Sessions 1966: 48. – Gaufin, Ricker, Miner, Milam and Hays 1972: 66.

Capnia coloradensis is known from the Rocky Mountain areas of Montana, Idaho, Wyoming, and Colorado in the United States, and from the Yukon, Canada. This is the first Saskatchewan record. The species has been collected (Fig. 177) from: Scarth River, Jct. Hwy. 120; Mackenzie Creek near Bow

River, Jct. Hwy. 165; Trapper Cabin Creek, Jct. Hwy. 120; Cub Creek, Jct. Hwy. 106; and McDougal Creek, Jct. Hwy. 120.

Diagnostic Characters. – Average length, males, 5.0 mm; females, 7.0 mm (from anterior margin of head to tip of folded wings). Males with narrow heavily sclerotized curved band on anterior margin of tergum 7 and median shining area behind it; latter flat in most specimens, but in Saskatchewan specimens with barely perceptible dark knob rising from it. Narrow dark band extended along anterior margin of terga 2–6, interrupted medially. Prominent hump on tergum 8 and supra-anal process long with conspicuous downturned lobe at apex. Sternum 9 without ventral lobe. Female sternum 7 moderately sclerotized, with many long, stout pale hairs on posterior half, sclerotization continuous across intersegmental groove. Subgenital plate with posterior margin small, rounded and with conspicuous subcuticular oval area visible in center; subgenital plate separated from lateral sclerotized areas of sternum 8 by narrow membranous area. The previously unknown nymph is described below.

Description. – Total length of mature nymph: 3.5–4.5 mm.

General color light brown, lighter ventrally; darker on borders of pronotum, anterior corners of meso- and metanota and anteriorly to lateral ocelli. Appendages and wing pads light yellow; no conspicuous color pattern. Maxillae as in Fig. 144.

Head mostly glabrous with few long setae on top of the head, longest about equal to half diameter of eye (Fig. 140).

Pronotum with few long bristles on anterior and posterior borders, with shorter bristles between. Wing pads with many short hairs. Legs with usual fringe of hairs on tibiae and tarsi; tibiae with short stout bristles below fringe. Outer surface of femur with many short bristles and a few interspersed longer ones.

Abdomen covered with short clothing hairs, and a few stout bristles on posterior tergal margins (Fig. 140). Cerci of usual type.

Ricker (1965), Gaufin *et al.* (1966) and Gaufin *et al.* (1972) figured the adult genitalia; drawings of the nymph are presented in Fig. 140 and 144.

Bionomics. – Gaufin *et al.* (1972) noted that adults of *Capnia coloradensis* emerge in March and April. In Saskatchewan, adults were collected on April 18, 1975 at Trapper Cabin Creek, Jct. Hwy. 120; May 29, 1975 at Cub Creek, Jct. Hwy. 106; April 12, 1976 at Mackenzie Creek, Jct. Hwy. 165 and on May 30, 1975 at McDougal Creek, Jct. Hwy. 120. Nymphs were absent from benthic samples after the spring adult emergence indicating a univoltine life history.

Capnia confusa Claassen
(Fig. 37, 54, 55, 70, 139, 142, 179)

Capnia nivalis, Neave 1929: 163.

Capnia confusa Claassen 1936: 623. – Hanson 1946: 238. – Jewett 1959: 43. – Gaufin, Nebeker and Sessions 1966: 47. – Gaufin, Ricker, Miner, Milam and Hays 1972: 67.

Capnia confusa is known from Alaska, Alberta and British Columbia, south to Utah, and east to Wyoming and Montana. This is the first Saskatchewan record, and the species has been collected (Fig. 179) from: North Fork of Scarth River, Jct. Hwy. 120; the stream at mile 83, Jct. Hwy. 106; Mackenzie Creek, near Bow River, Jct. Hwy. 109; River 40 mi. N. of Hudson Bay, Sask., Jct. Hwy. 109; and Waskwei River, Jct. Hwy. 109.

Ricker (1964) presented a North American distribution map of the species.

Diagnostic Characters. – Average length, males 5.5 mm; females, 7.5 mm (from anterior part of head to tip of folded wings). Males of this species closely resemble those of *Capnia vernalis*, but females of *Capnia confusa* and *Capnia vernalis* are markedly different. Male supra-anal process long, about 10 times longer than wide (Fig. 54), fairly uniform in width throughout its length and tip not down-turned in side view (Fig. 55). Humps absent from both terga 7 and 8. Sterna 7 and 8 of females not united by median sclerotized connection; posterior edge of sternum 7 membranous with narrow median sclerotized projection extended to or overlapping part of sternum 8 (Fig. 70). The first description of a nymph of this species is given below.

Description. – Total length of mature nymph: 4.5 – 6 mm.

General color light brown, lighter ventrally; darker on borders of pronotum, anterior corners of meso- and metanota and anteriorly to lateral ocelli. Appendages and wing pads yellow. Maxillae as in Fig. 142.

Head mostly glabrous with few long setae, longest about half diameter of eye (Fig. 139).

Pronotum with a few long bristles on anterior and posterior borders, and shorter bristles between meso- and metanota with a few long hairs extended anteriorly and shorter bristles on the disc; wing pads with many short hairs. Legs with usual fringe of hairs on tibiae and tarsi; tibiae with short stout bristles below fringe. Outer surface of femora with many short bristles and few interspersed longer ones.

Abdomen covered with short clothing hairs, and few stout bristles on posterior tergal margins (Fig. 39). Supra-anal lobe of male as in Fig. 139; cerci of the usual type.

I have been unable to distinguish the nymph of this species from the nymph of *Capnia coloradensis*.

Gaufin *et al.* (1966) figured the male and female genitalia; first figures of the nymph are presented in Fig. 139 and 142.

Bionomics. – Gaufin *et al.* (1972) noted that *Capnia confusa* nymphs are common in creeks and adults emerge in February to July. In Saskatchewan, adults were collected from the North Fork of Scarth River, Jct. Hwy. 120 on May 15, 1975, stream at mile 83, Jct. Hwy. 106 on April 26, 1976, Mackenzie Creek near Bow River, Jct. Hwy. 165 on April 16, 1976, and May 7, 1976, McDougal Creek, Jct. Hwy. 120, on May. 30, 1975, and from Waskwei River, Jct. Hwy 109 on June 11, 1975. Nymphs were absent from benthic samples after the adults emerged in spring, indicating a univoltine life history.

Capnia gracilaria Claassen
(Fig. 52, 53, 72, 138, 143, 177)

Capnia gracilaria Claassen 1924: 57. – Needham and Claassen 1925: 258. – Claassen 1940: 93. – Ricker 1943: 99. – Hanson 1946: 239. – Gaufin, Nebeker and Sessions 1966: 46. – Gaufin, Ricker, Miner, Milam and Hays 1972: 67.

Capnia gracilaria is known from British Columbia and Manitoba south to Oregon, Montana and Utah. This first Saskatchewan record is from Cypress Hills at Battle Creek near Reesor Lake (Fig. 177).

Diagnostic Characters. – Average length, males, 4.0 mm (from anterior portion of head to tip of folded wings); females, 7.5 mm. Males without conspicuous hump on tergum 8 but most specimens with low hump near anterior edge of tergum 7. Supra-anal process long (about 10 times longer than wide) and round in cross-section, extended to posterior edge of tergum 7 (Fig. 52). In lateral view, supra-anal process gently S-shaped and of same width throughout its length (Fig. 53). Female abdomen with very broad dorsal membranous stripe on segments 1 to 8. Subgenital plate of most specimens slightly anterior to membranous border of eighth sternum and set off laterally by weakly sclerotized areas; posterior edge of subgenital plate is usually straight or slightly rounded often with small median blunt protuberance, plate with 3-toothed appearance (Fig. 72). The nymph is described below for the first

time.

Description. – Total length of mature nymph: 5.0–6.5 mm.

General color light brown, reddish brown in very mature specimens, lighter ventrally, appendages and wing pads light yellow; no conspicuous color pattern.

Head mostly glabrous with a few long setae on top of head, longest about equal to diameter of the eye (Fig. 138). Galea of maxilla without definite fringe of hairs (Fig. 143).

Pronotum with few long bristles at anterior and posterior borders, and few short hairs between. Meso- and meta-nota with few long bristles anteriorly, and few stout bristles along notal discs; wing pads glabrous. Legs with usual fringe of hairs on tibiae and tarsi; tibiae with short stout bristles below fringe. Outer surface of femora with many short bristles and a few interspersed longer ones.

Abdomen with a few stout bristles on posterior tergal margins and a few short hairs along rest of each tergum (Fig. 138). Supra-anal lobe of male as in Fig. 138; cerci of usual type.

Needham and Claassen (1925) figured the male genitalia; Ricker (1943) illustrated the female genitalia. Gaufin *et al.* (1966) and Gaufin *et al.* (1972) figured both male and female genitalia. First nymphal figures are presented in Figs. 138 and 141.

Bionomics. – Gaufin (1972) noted that nymphs of this species are common in creeks and small rivers, with adult emergence occurring from January through May. In Saskatchewan, adults were collected at Battle Creek, Cypress Hills on April 20, 1975, March 28, 1976 and May 19, 1976. Nymphs were absent from benthic samples after the emergence of adults in spring indicating a univoltine life cycle.

Nebeker (1971c) studied the adult emergence of *Capnia graclaria* at altitudes of 2590 meters down to 1530 meters in the Wasatch Mountains, Utah. Emergence was found to be spread up to five months apart depending on altitude (i.e. temperature) for nymphs which received the same photoperiod.

Capnia vernalis Newport
(Fig. 56, 57, 67, 141, 178)

Capnia vernalis Newport 1848: 451. – Claassen 1931: 109. – Ricker 1938: 135. – Claassen 1940: 95. – Harden and Mickel 1952: 24. – Harper and Hynes 1971b: 938. – Hitchcock 1974: 45.

Published records of *Capnia vernalis* are from Alberta, Manitoba, Ontario, Labrador, Minnesota and Ohio. Although specimens were not collected in the present study and there are no published records of the species from Saskatchewan, W.E. Ricker (pers. comm.) has examined a female *Capnia vernalis* from this province, Saskatoon, Sask.; May 19, 1940; A.R. Brooks, coll. An additional female is deposited in the Biology Department Entomology Museum, University of Saskatchewan, Saskatoon, Saskatchewan, with the following collection data: Saskatoon, Sask.; April 24, 1918. The genitalia are shrivelled since this specimen has been pinned, but it appears very close to *Capnia vernalis*. The Saskatchewan distribution of this species is indicated in Fig. 178.

Diagnostic Characters. – Average length, males 4.5 mm; females, 6.5 mm (from anterior part of head to tip of folded wings). Male sternum 9 produced posteriorly into bluntly pointed subanal plate with elongate process at tip lying between subanal lobes; elongate process with second acute anterior projection dorsal to sternum. Subanal lobes each subacute and marked off from sternum by deep notch. Supra-anal process extended forward to hind margin of tergum 8 (Fig. 56); its distal one-third narrower in side view and the tip pointed (Fig. 57). Female subgenital plate with strongly sclerotized posterior lip about one-third width of sternum, and slightly anterior to its hind margin. Sclerotized floor of genital tract visible through exoskeleton (Fig. 67) anterad to posterior lip of subgenital plate. Sterna 7 and 8 connected by narrow sclerotized bridge.

Nymph with tip of galea of maxilla not evenly pointed, but expanded and covered with fringe of long hairs (Fig. 141).

Ricker (1938) figured the type specimens; Harper and Hynes (1971b) illustrated the adult genitalia, wings and nymph.

Bionomics. – There is no available biological information on this species.

Genus *Utacpnia* Nebeker and Gaufin

Nebeker and Gaufin (1965) studied the *Capnia columbiana* complex and reported 10 species in western and arctic America. Further study of this group and other North American *Capnia* resulted in recognition of subgeneric status for this complex under the name *Utacpnia* (Nebeker and Gaufin, 1967), and it was later assigned generic status by Zwick (1973).

Males vary from long-winged to apterous. There is no lobe on sternum 9. With the exception of wingless adults, postfurcasternal plates are partially fused to the spinasternum. The prothoracic spinasternum is fused at lateral angles to the mesothoracic basisternum by a connection four times longer than wide. The supra-anal process is bipartite with the upper part furcate and enlarged at its tip (Fig. 50, 51). Females have the subgenital plate bounded on either side by a well-defined lateral sclerotized plate with various median and anterior sclerotization (Fig. 69). Nymphs are poorly known and inseparable at present. One species of *Utacpnia* is known from Saskatchewan.

Utacpnia trava (Nebeker and Gaufin)

(Fig. 50, 51, 69, 178)

Capnia trava Nebeker and Gaufin 1965: 479.

Capnia (Utacpnia) trava, Nebeker and Gaufin 1967: 236.

Utacpnia trava, Zwick 1973: 392.

Utacpnia trava was previously reported from Montana and Idaho. This is the first Saskatchewan and Canadian record (Fig. 178). Specimens have been collected at Battle Creek, near Reesor Lake, Cypress Hills; Scarth River, Jct. Hwy. 120; Trapper Cabin Creek, Jct. Hwy. 120; and McDougal Creek, Jct. Hwy. 120.

Diagnostic Characters. – Average length: males, 7.5 mm (from anterior margin of head to end of abdomen); females, 8.5 mm (from anterior margin of head to tip of folded wings). Male genitalia with fan-shaped enlargement at tip of upper supra-anal process; lower process massive and greatly enlarged, about as wide as tips of upper process; posterior end of supra-anal process enlarged and notched in dorsal view (Fig. 50, 51). Females with anterior sclerotization of subgenital plate joined by continuous pigmentation from anterior sclerotization extended posteriorly to pigmented tip of subgenital plate; posterior margin notched (Fig. 69). Nymphs of this species are unknown.

Nebeker and Gaufin (1965) and Gaufin *et al.* (1972) illustrated the adult genitalia.

Bionomics. – Adults of this species are usually collected from February to April, but in one collection from a glacial lake emergence was July 11, 1964 as a result of the extremely cold water in which the nymphs lived (Nebeker and Gaufin, 1967). In Saskatchewan, adults were collected from McDougal Creek and Trapper Cabin Creek on April 18, 1975, and from Battle Creek, on April 2, 1975 and March 28, 1976.

Genus *Isocapnia* Banks

Compared to most capniines, specimens of *Isocapnia* are unique because of their large size and the rarity of their collection. Adults are characterized by basally straight veins R_1 and A_1 and the forewing, two or more crossveins in the costal area beyond the cord (Fig. 39), the mesothoracic furcasternum faintly demarked from the postfurcasternal plates with which it is united, metathoracic furcasternum united with and faintly demarked from the first abdominal sternum, and the prothoracic presternum broadly fused with the basisternum (Fig. 18). The known nymphs of *Isocapnia* differ from those of other stonefly species by long swimming hairs along the cerci (Fig. 26). Dwarf males occur in some *Isocapnia* species in which wings are very reduced (1–2 mm long) and the body is generally small. Though brachyptery is not rare in Plecoptera, Ricker (1959) noted that the unusual aspect of brachyptery in *Isocapnia* is the occurrence of extremely short-winged and completely long-winged individuals in the same population without intergradation.

Ricker (1959) established three well-defined North American species groups of *Isocapnia* for the eleven species known. These are the *grandis*, *hyalita*, and *abbreviata* species groups. One member of the *grandis* group and one member of the *hyalita* group occur in Saskatchewan.

Key to Saskatchewan species of *Isocapnia*

Adults

- | | | |
|----|--|----|
| 1 | Costal crossveins one to four before end of Sc, and none to two beyond it; male 9th tergum with prominent posterior notched or bilobed process; female subgenital plate without median recessed tongue set off by unsclerotized notch on either side (Fig. 66) | |
| | <i>Isocapnia missouri</i> Ricker p. | 33 |
| 1' | Costal crossveins four to eight before end of Sc, two to four beyond it (Fig. 39); no raised process on male 9th tergum (Fig. 63, 64); female subgenital plate with median recessed tongue set off by unsclerotized notch on either side (Fig. 65). | |
| | <i>Isocapnia crinita</i> (Needham and Claassen), p. | 32 |

Nymphs

Since the nymph of *Isocapnia missouri* is unknown, a nymphal species key is not provided.

Isocapnia crinita (Needham and Claassen)
(Fig. 26, 39, 62-65, 179)

Capnia crinita Needham and Claassen 1925: 269.

Isocapnia crinita, Claassen 1940: 96. – Frison 1942b: 69. – Hanson 1946: 239. – Ricker 1959: 643.

Isocapnia crinita has been reported from Colorado, Utah and Montana with this as the first Saskatchewan and Canadian record. It has been collected from Battle Creek, Cypress Hills (Fig. 179).

Diagnostic Characters. – Average length, males, 11.5 mm (from most anterior margin of head to tip of the folded wings); females, 15.0 mm. Male tenth tergum cleft dorsally, with posterior angle of cleft filled by broad, triangular, basal portion of supra-anal process; latter curved gently anterad and upward, with very short blunt tip extended abruptly anterad (Fig. 62–64). Females with dorsal unsclerotized stripe on terga 2–8; all sterna with heavily sclerotized areas anteriorly, broadly interrupted at midline. Sterna 1–6 with series of irregular dots on either side of midline, sternum 7 with two nonsclerotized areas posterolaterally. Subgenital plate situated slightly anteriorly to level of lateral margins of sternum; central sclerotized portion with margins more markedly sclerotized but pigment not extended to hind margin of plate (Fig. 65).

Male nymph with sheath of supra-anal process curved forward as in adult.

It is interesting that a single dwarf male of this species was collected at Battle Creek on May 19, 1976. Long-winged specimens were not collected. *Isocapnia crinita* can now be added to Ricker's (1959) list of *Isocapnia* species in which dwarfing is known to occur, leaving three species *abbreviata*, *grandis* and *mogila* in which only normal males are known.

Frison (1942a), Ricker (1959), and Gaufin *et al.* (1972) figured the male and female genitalia, Ricker (1959) figured the terminalia of the male exuviae.

Bionomics. – Specimens of *Isocapnia crinita* are rarely collected. Gaufin *et al.* (1972) state that in Montana adults emerge from March to May. A single female was found on June 3, 1975 at Battle Creek near Reesor Lake, Cypress Hills, and 15 females and one male were collected on May 19, 1976 at the same locality. Stanford and Gaufin (1974) reported nymphs of *Isocapnia crinita* in subterranean waters about four meters below and 50 meters laterally from the Tobacco and Flathead River channels in Montana. It appears that most of the two-year nymphal life cycle is spent in these hyporheic communities and only when nymphs are mature do they migrate to the surface waters and molt to adults. If a similar hyporheic community exists below Battle Creek, it would explain the absence of nymphs from benthic samples taken a month before adults were collected.

Isocapnia missouri Ricker
(Figs. 66, 178)

Isocapnia missouri Ricker 1959: 651. – Gaufin, Ricker, Miner, Milam and Hays 1972: 82. – Baumann, Gaufin and Surdick 1977: 80.

Isocapnia missouri is known from western United States in Montana and Utah. This first Saskatchewan (and Canadian) record is from Battle Creek near Reesor Lake (Fig. 178).

Diagnostic Characters. – Average length, females, 14.5 mm (from anterior margin of head to tip of folded wings), dwarf males, 9.5 mm (from anterior margin of head to end of abdomen). Wings with one to four costal crossveins before end of subcosta, and none to two (usually one) costal crossveins beyond it. Male genitalia with tergum 9 with prominent notched or bilobed process; supra-anal process long and uniformly slender from base to apex. Female subgenital plate entirely sclerotized, without median recessed sclerotized tongue set off by unsclerotized notch on either side (Fig. 66).

The nymph is unknown.

Ricker (1959) and Gaufin *et al.* (1972) figured the adult genitalia.

Bionomics. – Gaufin *et al.* (1972) reported emergence of adults of *Isocapnia missouri* from March to May in Montana. I collected four females at Battle Creek near Reesor Lake on May 19, 1976. Nymphs were not collected in sweep net samples on this date, nor on March 28, 1976.

Stanford and Gaufin (1974) reported collecting nymphs of *Isocapnia missouri* as well as of *Isocapnia crinita* in subterranean waters below two Montana rivers. Apparently most of the two-year nymphal life cycle is spent below the main river channel and mature nymphs migrate to the surface stream to molt to adults. A similar community probably exists below Battle Creek; this would explain the absence of nymphs from benthic collections.

Family Nemouridae

Nemouridae is the largest family of Plecoptera comprising 373 species occurring in North America, Eurasia and northern Africa. The family was established by Newman (1853) but Klapalek (1905) later arranged this group in four families: Nemouridae, Capniidae, Leuctridae, and Taeniopterygidae.

Needham and Claassen (1925) described one subgenus of Nemouridae. Ricker (1952) recognized 12 subgenera in North America, which were later ranked as genera by Illies (1966). Baumann (1975) revised the family for the world adding three new genera and a new subfamily.

Useful structures in generic definitions include clear, pigmented or banded wings, presence or absence of cervical gills, membranous or partly sclerotized cerci, and presence or absence of a lobe at the base of the male ninth sternum. Adults of this family have a slanting crossvein between the costa and vein R_1 of the forewing, the wings at rest folded flat over the body and the last article of the labial palp subcircular in lateral view. The male supra-anal process is fully sclerotized and anteriorly recurved in members of most taxa. Either the seventh or eighth sterna of female are produced to form the subgenital plate. Nymphs are distinguished by number, size and arrangement of body setae. Six genera of Nemouridae live in Saskatchewan.

Genus *Nemoura* Latreille

Baumann (1975) observed that species belonging to *Nemoura* are mainly in more northern regions. Males are distinguished by terminal hooks on sclerotized cerci (Fig. 79, 80) and females have a large pregenital plate (on the seventh sternum) (Fig. 89), with lightly sclerotized truncate cerci. Nymphs lack cervical gills. Four species occur in North America; one lives in Saskatchewan.

Nemoura rickeri Jewett (Fig. 79, 80, 89, 145, 146, 151, 183)

Nemoura rickeri Jewett 1971: 190. – Baumann 1975: 21.

Nemoura rickeri has previously been reported from two Alaskan localities only. This first Saskatchewan and Canadian report (Fig. 183) is from the following localities: Puskwakau River, Jct. Hwy. 106; Mackay Creek, Jct. Hwy. 2; stream 40 mi. N. of Hudson Bay, Sask., Jct. Hwy. 109; stream at Promontory Campground, 15 mi. N. of La Ronge, Sask., Jct. Hwy. 2; and the stream at mile 5, Jct. Hwy. 165.

There is some question whether *Nemoura rickeri* is conspecific with the Palearctic *Nemoura sahlbergi* Morton, but it could be considered a valid species until a detailed study of all northern species is completed (R.W. Baumann, pers. comm.).

Diagnostic Characters. – Average length, males, 7.5 mm (from anterior portion of head to tip of folded wings); females, 9.0 mm. Male cerci strongly sclerotized on outer surface, directed upward; cercal tips each with outwardly directed, sharply pointed hairy tooth. Male genitalia with tenth tergum deeply incised medially; epiproct recurved, massive, and rectangular, in dorsal view tip blunt and twice as long as wide, but in lateral view tip is bluntly pointed; paraprocts simple and broad (Fig. 79, 80). Female seventh sternum produced over most of sternum eight in form of broad rounded plate, hairy and heavily sclerotized along border; ninth sternum with small median plate extended anteriorly to margin of extended seventh sternum (Fig. 89). Since the nymph of this species has not previously been known, a detailed description follows.

Description. – Total length of mature nymph: 5.5–8.0 mm.

General color medium to light brown, underside very light brown; thin white ecdysial line the only marking. Head with dark brown subtriangular spots just behind antennae. Antennae light brown, first three articles dark brown; femora light brown, tibiae and tarsi slightly darker; cerci light brown, first five articles darker; each cercal article with dark band at base, width about one-fifth length of article.

Head with numerous short stout bristles slightly longer behind eyes and with a few long hairs on

anterior region of head.

Pronotum trapezoidal, wider anteriorly, and with short dorsal bristles and pronotal fringe (Fig. 146); meso- and meta-nota with numerous short stout bristles longer at anterior corners.

Legs with numerous short stout bristles; no tibial fringe but several long hairs along length of tibial margin; femora in side view about four times as long as wide (Fig. 145).

Abdomen with numerous short stout bristles with marginal bristles longer, up to one-third tergal length. Tenth abdominal tergum of mature male nymph with distinct pattern (Fig. 148). Cercal bristles in regular whorls, bristle length between one-quarter and one-half that of cercal article (Fig. 151).

Until comparative study is made of nymphs of *Nemoura*, it is impossible to identify distinguishing characters of *Nemoura rickeri* nymphs.

Bionomics. – In Alaska, *Nemoura rickeri* specimens were collected on June 30, 1968. Saskatchewan collection dates for adults are: Puskwakau River, Jct. Hwy. 106, June 10, 1975, and May 30, 1976; stream 40 mi. N. of Hudson Bay, Sask., June 11, 1975; stream at mile 5, Hwy. 165, May 29, 1975; and stream at Promontory Campground, 15 mi. N. La Ronge, Sask., June 21, 1976. The species appears to have an extended emergence because a large series of nymphs collected at the stream 15 mi. N. of La Ronge, Sask. showed a wide variation in wing pad development from very mature to having wing pads just beginning to form.

Genus *Podmosta* Ricker

This genus is characterized by absence of cervical gills, simple male cerci and a male supra-anal process which is short, thick, slightly curved, complex in structure and mostly membranous. The male tenth tergum has a deep median depression (Fig. 76). The female seventh sternum is unmodified, but the eighth sternum is produced into a subgenital plate which is straight or excavated posteriorly and usually slightly notched. There is a distinct darkly sclerotized stripe along the midline of the subgenital plate (Fig. 90). Five North American species of *Podmosta* are known and one is found in Saskatchewan.

Podmosta delicatula (Claassen) (Fig. 76, 90, 150, 152, 182)

Nemoura delicatula Claassen 1923: 285. – Claassen 1940: 54.

Nemoura (Podmosta) delicatula, Ricker 1952: 43. – Jewett 1959: 33.

Podmosta delicatula, Illies 1966: 219. – Baumann 1973: 92.

Podmosta delicatula is known from the Rocky Mountain areas of North America including British Columbia, California, Colorado, and Utah. First Saskatchewan records (Fig. 182) include Battle Creek, Cypress Hills near Reesor Lake; Shuard Creek, 11 mi. S. of Piapot, Sask.; and Bear Creek 10 mi. S. of Piapot, Sask.

Diagnostic Characters. – Average length, males, 5.5 mm (from anterior margin of head to tip of folded wings); females, 7.0 mm. Male genitalia with supra-anal process divided into long narrow ventral portion and short broad dorsal portion, with two thin, forked, sclerotized processes at apex of dorsal process (Fig. 76). Females with seventh sternum unmodified, and with median sclerotized stripe of eighth sternum three to four times as long as its greatest width and of fairly uniform width throughout its length; margin of eighth sternum with tiny median notch (Fig. 90). Since the nymph of this species has not previously been known, a detailed description follows.

Description. – Total length of mature nymph: 4.0–5.5 mm.

Color light brown; head darker, especially anterior to lateral ocelli, white markings extend from ecdysial line to tip of abdominal terga. Head with central light spot between lateral ocelli extending anteriorly about halfway between lateral ocelli and median ocellus. Antennae golden-brown; scape and pedicel darker. Cerci very light brown; lower half of each cercal article slightly darker.

Head covered with very short setae; ocelli form an equilateral triangle.

Pronotum narrower than head, trapezoidal, narrowed posteriorly with numerous short bristles; short setae extended over mesonotum and metanotum. Legs with short bristles; a few long hairs on tibiae, longest about equal to greatest width of tibiae. No tibial fringe.

Abdomen with numerous very short setae, largest bristles about one-quarter mid-dorsal tergum length. Each dorsal abdominal segment with distinct row of bristles along its posterior margin (Fig. 150). Whorls of cercal bristles at base of each cercal article, longest about one-third article length; dorsal and ventral bristles longer on distal cercal articles, where they may be 0.50–0.75 article length (Fig. 152).

The distinguishing characters of the nymph of this species cannot be specified now.

Needham and Claassen (1925) and Gaufin *et al.* (1972) figured the male and female genitalia. The first illustrations of nymphs are presented in Fig. 150 and 152. *Podmosta delicatula* is closely related to the eastern species *Podmosta macdunnoughi* (Ricker) but differs by not having the male dorsal process bent near its middle.

Bionomics. – Gaufin *et al.* (1972) state that the species is common in creeks and rivers throughout its range with adult emergence occurring from April to August. In Saskatchewan, adults were collected from Battle Creek, Cypress Hills near Reesor Lake on June 3, 1975, June 23, 1975, and July 13, 1975; from Bear Creek, 10 mi. S. of Piapot, Sask., on May 17, 1975; and from Shuard Creek, 11 mi. S. of Piapot, Sask. on June 3, 1975, June 23, 1975 and May 19, 1976. Nymphs were absent from benthic samples after the spring adult emergence, suggesting a univoltine life history.

Genus *Zapada* Ricker

Specimens of *Zapada* are commonly encountered, especially in western North America. Adults generally emerge in early spring. Males have large angular outer paraproctal lobes and a short broad epiproct with a well developed dorsal sclerite (Fig. 74). The female seventh sternum is slightly produced over an unsclerotized eighth sternum (Fig. 86). The four cervical gills are unbranched except in *Zapada cinctipes* whose specimens have four to five branches.

Nymphs have whorls of large spines on all femora. Seven North American species are known; one in Saskatchewan.

Zapada cinctipes (Banks) (Fig. 10, 11, 14, 74, 86, 183)

Nemoura cinctipes Banks 1897: 21. – Needham and Claassen 1925: 212. – Claassen 1940: 53.

Nemoura (Zapada) cinctipes, Ricker 1952: 57. – Jewett 1959: 35. – Gaufin, Ricker, Miner, Milam and Hays 1972: 41.

Zapada cinctipes, Illies 1966: 250. – Baumann 1975: 31. – Baumann, Gaufin and Surdick 1977: 42.

Zapada cinctipes is common in western Canada and United States from Alaska to California and Utah and east to Manitoba, South Dakota, Montana and Ohio. This first Saskatchewan report (Fig. 183) is based on material from the following localities: stream 80 mi. N. of La Ronge, Sask., Jct.

Hwy. 102; stream 39 mi. N. of Hudson Bay, Sask., Jct. Hwy. 109; Broad Creek, Jct. Hwy. 104; stream at Otter Lake, Missinipi, Jct. Hwy. 2; Mackay Creek, Jct. Hwy. 2; Caribou Creek, Jct. Hwy. 106; north fork of Scarth River, Jct. Hwy. 120; Mackenzie Creek near Bow River, Jct. Hwy. 165; Cub Creek, Jct. Hwy. 106; Battle Creek, Cypress Hills, near Reesor Lake; and east block of Cypress Hills Provincial Park, stream one-third mi. W. of Park Gates.

Diagnostic Characters. – Average length, males, 9.5 mm (from anterior part of head to tip of folded wings); females, 13 mm. Adults with four groups of branched gill remnants, membranous cerci and wings with dark, transverse bands. Male genitalia with subanal lobes broad with short spine-like processes on inner margins; supra-anal process recurved, largely membranous and spinulose on outer halves (Fig. 74). Female seventh sternum produced over entire eighth sternum as a broadly rounded subgenital plate (Fig. 86).

Nymphs with distinct transverse line of bristles on femora; cervical gills with 4–5 branches.

Needham and Claassen (1925) and Jewett (1959, 1960) figured the adult genitalia. Castle (1939) described the nymph.

Bionomics. – Emergence of *Zapada cinctipes* is regulated by an initial photoperiodic response and a temperature stimulus (Nebeker, 1971c).

Clifford (1969) found that while most adults emerged in early spring after ice started breaking up in the Bigoray River, Alberta, some nymphs had molted to adults while the stream was still completely ice-covered. These were found in air spaces between the ice and water. Early-instar nymphs were first collected in samples in late June, and growth was steady throughout fall and winter. The life history was univoltine.

At Battle Creek, near Reesor Lake, Cypress Hills, adults and mature nymphs were collected in this study on March 28, 1976, and adults were still abundant, though no nymphs were found, on May 19, 1976.

Genus *Amphinemura* Ris

Adults of this genus are characterized mainly by the presence of cervical gill remnants and unmodified cerci. Male subanal lobes are divided into two narrow parts which may be recurved forward alongside the supra-anal process. Usually both inner and outer parts bear few to many heavy spinules (Fig. 77, 78). The female seventh sternum is produced about halfway over sternum 8 which bears a median notch and may be produced (Fig. 88). Nymphs have branched prosternal gills (Fig. 12). Ten North American species are known, and one occurs in Saskatchewan.

Amphinemura linda (Ricker)

(Fig. 12, 77, 78, 88, 182)

Nemoura (*Amphinemura*) *linda* Ricker 1952: 22.

Amphinemura linda, Illies, 1966: 181. – Baumann, Gauvin and Surdick 1977: 26.

Amphinemura linda is a common species in Canada and northern United States. Previous records include British Columbia, Alberta, Manitoba, Quebec, Ontario, Labrador, and Michigan. This first Saskatchewan record fills in the central Canadian distributional gap for the species. Specimens have been collected in the following localities (Fig. 183): Mistohay Creek, Jct. Hwy. 226; Nemeiben River, Jct. Hwy. 2; stream 10 mi. E. of Squaw Rapids Power Station; stream 80 mi. N. of La Ronge, Sask., Jct. Hwy. 102; stream 85 mi. N. of La Ronge, Sask., Jct. Hwy. 102, Mackay Creek, Jct. Hwy. 2; Nipekamew River, Jct. Hwy. 165, stream 37 mi. N. of Green Lake Sask., Jct. Hwy. 155; stream at mile

98, Jct. Hwy. 155; creek between Bedard Creek and Bisset Creek, Jct. Hwy. 106; Puskwakau River, Jct. Hwy. 106; creek at mile 135, Jct. Hwy. 106; Swan River, Jct. Hwy. 8; and the stream at mile 34 on the Wollaston Lake Road.

Diagnostic Characters. – Average length, males 6.5 mm (from anterior margin of head to tip of folded wings); females, 8.5 mm. Male genitalia with anterior lobe on sternum 9 and posterior projection; subanal lobes double with both branches bearing spines, most specimens with two spines on outer branch, and four to five on inner branch (Fig. 77); subanal lobes not recurved forward, and usually seen only in ventral view (Fig. 78); supra-anal process mainly membranous with sclerotized sides. Female seventh sternum produced halfway over sternum 8, and subgenital plate sclerotized and sinuate (Fig. 88).

Nymphs with long and pointed pronotal bristles; cercal bristles at least three-quarters length of each cercal article; and large femoral and tibial bristles darker in color than rest of leg.

Ricker (1952) figured the adult genitalia, and Harper and Hynes (1971d) illustrated the nymph.

Bionomics. – Harper (1973b) noted that *Amphinemura linda* was an autumnal species in which the first adults were found in late August and adult emergence was extended throughout September. The emergence pattern of males and females was similar, but males emerged earlier than females. The intensity of emergence was about the same throughout. Oviposition occurred mainly at midday and early afternoon of late September and early October.

The life history of *Amphinemura linda* was shown to be univoltine (Harper, 1973b). Eggs hatched in the laboratory under simulated stream conditions showed a short initial development in October, embryonic diapause for five months in winter and resumed development in March. Hatching occurred in April. Nymphal growth was continuous throughout the summer and ended just before emergence of adults. In one river with warm winter water temperatures, embryonic diapause lasted only two months although emergence occurred about the same time. This slower summer growth was due to a cooler summer stream temperature.

In Saskatchewan, *Amphinemura linda* emerges in July and August. Adults were collected from the creek between Bedard Creek and Bisset Creek, Jct. Hwy. 106 on July 2, 1975, from Puskwakau River, Jct. Hwy. 106 on July 17, 1975, from the stream at mile 98 near Ile-a-la-Crosse, Sask. on July 10, 1975, and from Mistohay Creek, Jct. Hwy. 226 on August 12, 1975.

Genus *Shipsa* Ricker

Adults of this genus have banded wings, unmodified cerci and lack cervical gills. The male tenth tergum is produced into long terminal projections with one on each side of the epiproct. The epiproct is modified by having the ventral sclerite extending to the dorsal surface and it terminates in a prominent forcep-shaped structure (Fig. 75). The female seventh sternum is produced and laterally excavated with the produced part of sternum 7 attached basally to sternum 8. The eighth sternum is not produced (Fig. 87). Nymphs have a fringe of long hairs along the posterior margins of the tibiae.

Shipsa rotunda (Claassen)

(Fig. 75, 87, 183)

Nemoura rotunda Claassen 1923: 290. – Needham and Claassen 1925: 219. – Harden and Mickel 1952: 17.

Nemoura (Shipsa) rotunda, Ricker 1952: 50.

Shipsa rotunda, Illies 1966: 247.

Shipsa rotunda, the single known species of this genus, has been reported from Alaska, Saskatchewan, Ontario, the Maritimes and eastern United States. Ricker (1944) reported the species from Black Lake, Saskatchewan and additional collection records include (Fig. 183): Little Red River, Prince Albert, Sask.; Nipekamew River, Jct. Hwy. 165; Mackay Creek, Jct. Hwy. 2; stream at south end of Wollaston Lake, Jct. Hwy. 105; Torch River, Jct. Hwy. 106; North Saskatchewan River, Jct. Hwy. 5; and North Saskatchewan River at Prince Albert, Sask.

Diagnostic Characters. – Average length, males, 7.5 mm (from anterior part of head to tip of folded wings); females, 10.5 mm. Since this is the only known species of *Shipsa*, generic characters also define specific characters.

Needham and Claassen (1925) figured the adult genitalia; Harden and Mickel (1952) illustrated nymphal characters.

Bionomics. – Harper (1973b) reported collecting early-instar nymphs of *Shipsa rotunda* in November in a southern Ontario stream. Growth was rapid and without arrest throughout the winter even though the stream had a thick ice cover. Nymphal development was complete by mid-April, about one week before adult emergence.

In Saskatchewan, *Shipsa rotunda* was most abundant at the North Saskatchewan River at Hwy. 5 (Borden Bridge). Mature nymphs were collected on April 25, 1974, May 2, 1974, and May 4, 1974. Adults were collected on May 4, 1974.

Genus *Malenka* Ricker

This common western North American genus is characterized by the presence of mesobasal lobes on male cerci (Fig. 73), a nipple-like ventral projection on the female seventh sternum and a notch on the posterior margin of the female eighth sternum (Fig. 85). Nymphs have four branched cervical gills. Eleven species are known in North America; one occurs in Saskatchewan.

Malenka californica (Claassen) (Fig. 76, 90, 147, 149, 153, 182)

Nemoura californica Claassen 1923: 284. – Frison 1942a: 261.

Nemoura lobata, Frison 1936: 260.

Nemoura (Malenka) californica, Ricker 1952: 33. – Jewett 1959: 32. – Gaufin, Ricker, Miner, Milam and Hays 1972: 32.

Malenka californica, Illies 1966: 191.

This species has been recorded mainly from the cordillera including New Mexico and California north to British Columbia and western Alberta. This first Saskatchewan report (Fig. 183) is from the following localities: Broad Creek, Jct. Hwy. 104; Mackenzie Creek, Jct. Hwy. 165; Waskwei River, Jct. Hwy. 109; and Scarth River, Jct. Hwy. 120.

Diagnostic Characters. – Average length, males, 8.0 mm (from anterior margin of head to tip of folded wings); females 8.5 mm. Male cercus with mesobasal lobe sclerotized, sharply pointed, and directed inward and backward. Male genitalia with outer part of subanal lobes broad and with notch on mesal margin (Fig. 73). Female seventh sternum with erect nipple-like protuberance on produced portion with its base anterior to hind margin of sternum; sternum 8 notched about halfway across and with no margin of extra sclerotization (Fig. 85). The nymph is described below for the first time.

Description. – Total length of mature nymph: 5.0–6.5 mm.

Color medium brown; antennae a little darker; legs brown; bristles on legs slightly darker than

ground color of leg; cerci pale.

Short bristles covering head capsule, those behind eyes longer and stout. Antennal bristles large near base but very small and short near tip.

Pronotum rectangular, covered with short bristles and hairs. Pronotal fringe well-defined consisting of long pointed bristles which are long on corners but very short along medial margin (Fig. 147). Meso- and metanota covered with medium-sized bristles especially on anterior corners. Legs with long stout bristles, the longest femoral bristles equal to about two-thirds of greatest femoral width; no tibial fringe of hairs but profuse tibial bristles.

Prosternal gills in four tufts; each tuft of 6–8 filaments forming a whorl about a central axis.

Abdomen with numerous long bristles, longest about 1.3 times as long as mid-dorsal length of corresponding tergum (Fig. 149). Whorls of cercal bristles regular; length of bristles equal to total length of cercal article (Fig. 153).

The nymph of this species is almost identical to that of *Amphinemura linda*, but if the two are compared there are several distinguishing features. *Amphinemura linda* has an overall orange-red color, while *Malenka californica* is brown. The body bristles of *Malenka californica* are much darker than the body; in *Amphinemura linda*, the bristles, especially the leg bristles, are only slightly darker than the body. The two species are also temporally separated. *Amphinemura linda* is a mid- to latesummer species with mature nymphs occurring in mid-July. However, *Malenka californica* is a fall species with mature nymphs occurring in late August.

Needham and Claassen (1925), Jewett (1959) and Gaufin *et al.* (1972) figured the male and female genitalia. Nymphal characters are illustrated in Fig. 147, 149 and 153.

Bionomics. – *Malenka californica* is found in small streams, creeks and small springs. Adults emerge in late summer or fall (Baumann, 1975), as soon as there is a sharp decrease of stream temperature (Nebeker, 1971c).

In Saskatchewan, adults have been collected on August 8, 1975 at Mackenzie Creek, Jct. Hwy. 165, September 1, 1975 at Waskwei River, Jct. Hwy. 109, and on September 25, 1975 at Scarth River, Jct. Hwy. 120. Adults of this species have been found in stomachs of brook trout at Scarth River (D. Larson, pers. comm.).

Nymphs were not present in samples taken at Mackenzie Creek, Jct. Hwy. 165 in April or May of 1976. However, early instar nymphs were collected at the same locality on June 25, 1975. There is probably an embryonic diapause over the winter and early spring, with the main nymphal development occurring throughout June, July, and early August.

Family Leuctridae

Leuctridae are characterized by having wings rolled around the body at rest, cu-m and intercubital crossveins in the forewings, a forked cubitus and simple media in the hindwings of most genera, single articulated cerci (simple in most genera), an inconspicuous male epiproct and absence of gills. Male leuctrids are unique by having a long median process or subanal probe between the paraprocts (Ricker and Ross, 1969). Nymphs have the first tarsal article longer than the second, hindwing pads subparallel to the body axis, and the first six or less abdominal segments divided into tergum and sternum by a membranous fold. The family occurs in North America, Eurasia and northern Africa.

At present, the nomenclature of Leuctridae is somewhat confused. Hanson (1941) proposed the genus name *Paraleuctra* for seven North American species previously in the genus *Leuctra*. Frison (1942a), Ricker (1943, 1952), Jewett (1956, 1959, 1960) and Gaufin *et al.* (1972) considered *Paraleuctra* a subgenus of *Leuctra*, but Illies (1966) maintained the generic status of *Paraleuctra*, this was accepted

by Ricker and Ross (1969) and Hitchcock (1974). I follow the nomenclature of Illies (1966). Both *Leuctra* and *Paraleuctra* occur in the province but the other North American genera of this family, *Perlomyia*, *Megaleuctra* and *Zealeuctra*, were not found.

Genus *Leuctra* Stephens

Adults of *Leuctra* differ from the closely related genera *Paraleuctra* and *Zealeuctra* by having the m-cu crossvein in the hindwing proximal to the dichotomy of Cu₁, and Rs and M originating from different points on the radius (Fig. 36). Male cerci are unmodified. The number and shape of processes on the male seventh and eighth terga are often used for species determinations. Nymphs differ from other genera because the first four abdominal segments are divided into tergum and sternum by a membranous fold (Fig. 27), and labial palpi extend well beyond the paraglossae (Fig. 21).

Members of this genus seem to prefer smaller streams (Hitchcock, 1974). The adults are small, brownish and inconspicuous. Of 22 North American species, one species of *Leuctra* was collected in Saskatchewan, *Leuctra ferruginea*.

Leuctra ferruginea (Walker) (Fig. 21, 27, 36, 84, 92, 184)

Nemoura ferruginea Walker 1852: 183.

Leuctra decepta, Claassen 1923: 260. – Claassen 1940: 77. – Frison 1942a: 257. – Harden and Mickel 1952: 21.

Leuctra ferruginea, Illies 1966: 87. – Hitchcock 1974: 76.

Leuctra ferruginea ranges from eastern Canada (Ontario, Quebec, Newfoundland, Nova Scotia, and New Brunswick), eastern United States (Maine to Florida) to Illinois and Minnesota in the west. The new Saskatchewan record is the most western extension of the species range. Specimens were collected from the following localities (Fig. 183): stream 85 mi. N. of La Ronge, Sask., Jct. Hwy. 102; Broad Creek, Jct. Hwy. 104; stream at mile 30 on the Wollaston Lake Road; Mackay Creek, Jct. Hwy. 2; Low Creek, Jct. Hwy. 104 and Waddy River, Jct. Hwy. 102.

Diagnostic Characters. – Average length, males, 6 mm (from anterior margin of head to tip of folded wings); females, 8.5 mm. Male genitalia with subanal lobes slender and considerably longer than specilla; supra-anal lobe broadly rounded and cerci unmodified, small raised process on eighth abdominal tergum in most specimens, but in some individuals missing (Fig. 84). Some specimens with dark sclerotization on tergum 7 which resembles a process but not raised. Female sternum 8 produced into broad and deeply notched subgenital plate which reaches nearly halfway across sternum 9, two rounded lobes of subgenital plate separated by membranous tissue (Fig. 92).

Nymphs with all abdominal terga covered with short stout bristles but no stout bristles on abdominal sterna.

Needham and Claassen (1925), Frison (1942a) and Hitchcock (1974) figured the adult genitalia; Claassen (1931) and Harper and Hynes (1971a) figured the nymph.

Bionomics. – Harper and Hynes (1971a) noted that *Leuctra ferruginea* occurs predominantly in small cold streams although it may be found in a wide variety of streams and even small warm rivers. Harper (1973b) found that adult emergence in southern Ontario was extended, lasting from early May to September of 1968, although the majority of individuals emerged in late May and early June. Males emerged slightly earlier than females. Adult feeding began soon after emergence but mating did not occur for a few days. Oviposition was observed in the field from mid-June until mid-October. Each

egg batch contained an average of 204 eggs. Females produced an average of 26 egg batches.

Eggs maintained at a constant temperature of 10 C and photoperiod of 12 hours light; 12 hours darkness hatched in 49 days (Harper, 1973b). There was no evidence of embryonic diapause. Cooler temperatures lengthened embryonic development; therefore, eggs laid in mid-October would not hatch until spring.

Nymphal growth and emergence appeared to depend upon water temperatures. Only newly hatched nymphs were collected from October to May in streams coldest in summer and warmest in winter. Nymphs hatching in October grew rapidly in fall but little growth occurred during winter. Some of these nymphs emerged in late summer, but the majority of the population was only half grown by the end of the summer and did not emerge until the following year. Growth continued until October, slowed for winter, and resumed in March. Most nymphs matured in May and June. The number of individuals which completed their nymphal growth in one year was very small; most required two years.

A semivoltine growth pattern was still apparent in the warmest stream where *Leuctra ferruginea* was common, but in this case a large part of the population was univoltine. Adult emergence was short and late (most mature nymphs were collected in July).

It is not known whether the life history of this species is univoltine or semivoltine in Saskatchewan. Adults were collected on July 4, 14, and August 7 of 1974 from the stream 85 mi. N. of La Ronge, Sask., Jct. Hwy. 102. This was the only Saskatchewan stream sampled where the species was abundant.

Genus *Paraleuctra* Hanson

Paraleuctra differs from other leuctrid genera in having the m-cu crossvein reach Cu₁ after it has divided (Fig. 34), heavily sclerotized male cerci (Fig. 83), the male ninth tergum entire and the female dorsum with a longitudinal sclerotized stripe on either side. Nymphs have labial palpi extending to the tip of the paraglossae, the first six abdominal segments divided into tergum and sternum by a membranous fold, and the subanal lobes not partly fused but separate. Eight species are known in North America and one occurs in Saskatchewan.

Paraleuctra vershina (Gaufin and Ricker) (Fig. 34, 81-83, 91, 184)

Leuctra occidentalis, Needham and Claassen 1925: 231.

Paraleuctra occidentalis, Hanson 1941: 57. – Jewett 1959: 39 and 1960: 141. – (in part) Illies 1966: 114.

Paraleuctra occidentalis auct., Hanson 1962: 135.

Paraleuctra vershina Gaufin and Ricker 1974: 285.

Paraleuctra vershina ranges from the cordilleran regions of Canada and the U.S. (British Columbia, Alberta, California and Washington) and east to Colorado, Montana and Utah. This, the first Saskatchewan record, is from Battle Creek near Reesor Lake (Fig. 184).

Diagnostic Characters. – Average length, males 6.0 mm (from anterior margin of head to tip of folded wings); females, 8.0 mm. Male genitalia with tergum 10 partly cleft; supra-anal lobe triangular and bearing slender, recurved, whip-like process at tip (Fig. 81, 82); cerci modified into chitinous armed processes, bulbous at base and each bearing sharp tooth above and below (Fig. 83); subanal lobes modified into probe with each lobe receding into ninth segment. Female subgenital plate produced into two lobes lined with long hairs and separated by a broad notch (Fig. 91). Nymphs of this species are unknown.

Needham and Claassen (1925) illustrated the adult genitalia. Hanson (1962) figured the male cerci

showing the characters which distinguish *Paraleuctra vershina* from other *Paraleuctra*.

Bionomics. – Little is known of the biology of this species. In Battle Creek adult specimens were collected on June 23, July 13, and July 20, 1975.

Family Chloroperlidae

Chloroperlidae are small to medium size stoneflies characterized by having paraglossae much longer than glossae, gills absent, three ocelli, reduced wing venation (only two anal veins) and a small or absent anal area in the hindwing. The family is found in North America, eastern and western Asia and Europe. Male genitalia have unmodified paraprocsts and a well developed epiproct. The male tenth tergum is cleft and lobes are absent from all male sterna. Female subgenital plates are variable.

Nymphs lack anal gills, have cerci about three-quarters the abdominal length, and have hindwing pads subparallel to the axis of the body. The last article of each nymphal maxillary palp is abruptly thinner than previous segments.

In North America, Chloroperlidae presently consists of two subfamilies, ten genera, and about 56 species. The subfamily Paraperlinae of western North America is comprised of the genera *Utaperla* Ricker and *Kathroperla* Banks which are monotypic and the genus *Paraperla* Banks with two species. The subfamily Chloroperlinae, of eastern and western North America, originally consisted of three genera: *Hastaperla* Ricker, *Chloroperla* Newman and *Alloperla* Banks. The five subgenera of *Alloperla* have recently been assigned full generic status (Illies, 1966).

Three genera of Chloroperlinae are known in Saskatchewan: *Hastaperla*, *Suwallia* and *Triznaka*.

Genus *Hastaperla* Ricker

Adults of *Hastaperla* are distinguished from other chloroperlid genera by the lack of a fold separating the anal area from the remainder of the hindwing. The anal cell of the forewing gives rise to a single unbranched vein (Fig. 32). Nymphs of *Hastaperla* cannot be distinguished from *Chloroperla*; both have the inner margins of the hindwing pads straight and mature larvae are 7 mm in length or less. Of the three species of *Hastaperla* known in North America, one lives in Saskatchewan.

Hastaperla brevis (Banks) (Fig. 32, 93, 96, 185)

Chloroperla brevis Banks 1895: 314.

Hastaperla calcarea, Ricker 1935: 200.

Hastaperla brevis, Claassen 1940: 197. – Frison 1942a: 340. – Harden and Mickel 1952: 62. – Ricker 1964: 54. – Hitchcock 1974: 168.

Hastaperla brevis is the most widespread species of Chloroperlidae (Gaufin, 1964), ranging from Nova Scotia through New England, south to Georgia, and west to Oklahoma and Manitoba. Though not previously reported in Saskatchewan new collection records (Fig. 185) for the province include: South Saskatchewan River at the ferry North of Birch Hills, Sask.; Weyakwin River, Jct. Hwy. 2; Ballantyne River, Jct. Hwy. 106; Mackenzie Creek, Jct. Hwy. 165; Bow River, Jct. Hwy. 165; Nipekamew River, Jct. Hwy. 165; Red Deer River, Jct. Hwy. 8; Waskwei River, Jct. Hwy. 109; McDougal Creek, Jct. Hwy. 120; Puskwakau River, Jct. Hwy. 106; Torch River, Jct. Hwy. 106; stream at mile 83, Jct. Hwy. 106; Waddy River, Jct. Hwy. 102; Overflowing River, Jct. Hwy. 109; Crean River, Jct. Hwy. 2; Pine Creek, Jct. Hwy. 165; Cluff Creek near Cluff Lake; Churchill River at Wintego Lake

rapids; Mackay Creek, Jct. Hwy. 2; Fond du Lac River at Black Lake; and Montreal River Jct. Hwy. 2.

Diagnostic Characters. – Average length, males, 6.5 mm (from anterior margin of head to tip of folded wings); females, 9.0 mm. Male genitalia with ninth abdominal segment produced ventrad, rounded and hairy behind, with penis lying beneath; curved chitinous process on each side of penis joined at posterior end to form blunt, prong-like tip (may be conspicuous only in cleared-mount); male epiproct rounded (Fig. 93). Female subgenital plate produced over most of ninth sternum, triangular and rounded at tip (Fig. 96).

Nymphal hindwing pads subparallel to axis of body and inner wing pad margins straight; cerci three-quarters abdominal length; mature larvae 7 mm in length or less (from anterior tip of head to end of abdomen).

Adult genitalia have been figured by Needham and Claassen (1925), Ricker (1935), Frison (1935, 1942a) and Gaufin *et al.* (1966); nymphs were illustrated by Frison (1935). Adults differ from the closely related species, *Hastaperla orpha* (Frison) by lacking a dorsal abdominal stripe.

Bionomics. – Harper and Magnin (1969) studied the life cycle of *Hastaperla brevis* in Quebec. Adult emergence began in June, with the period of time for egg laying and hatching being relatively short. Nymphs were first collected in October, and growth was rapid during fall and early winter but slow in January. In May growth continued and maximum size was reached. It was concluded that growth was not closely synchronized since nymphs in various stages of maturity were collected in each sample. Though Hitchcock (1974) stated that the nymphs were herbivorous, Harper and Magnin (1969) contended that nymphs were at least partly carnivorous.

Genus *Suwallia* Ricker

Males of this genus are characterized by having slender, curved finger-like processes developed from the basal article of the cerci. The male supra-anal body is a membranous lobe with a small hairy process at its tip (Fig. 95). Adults have a small anal lobe on the hindwing, a dark dorsal stripe on the abdomen, and dark U-marks on the meso- and metanota. Few nymphs of *Suwallia* have been described, so nymphal generic characters are not defined.

Suwallia lineosa (Banks) (Fig. 95, 98, 163, 165-167)

Alloperla lineosa Banks 1918: 7. – Claassen 1940: 186. – Ricker 1964: 68.

Alloperla (Suwallia) lineosa, Ricker 1943: 139. – Jewett 1955: 151. – Gaufin 1964: 42.

Suwallia lineosa, Illies 1966: 449.

Suwallia lineosa occurs in the Rocky Mountains of western Canada (British Columbia and Alberta) and westward to the Cascade and Wallowa Mountains (Colorado, Montana, Oregon, Washington, Wyoming). Though not previously reported in Saskatchewan, specimens were collected in Cypress Hills at Battle Creek near Reesor Lake (Fig. 185). It was not collected further downstream in Battle Creek near Consul, Sask.

Diagnostic Characters. – Average length, males, 7.8 mm (from anterior margin of head to tip of folded wings); females, 8.9 mm. Adult without head or pronotal markings except for ocellar rings and faint stripe in centre of pronotum (Fig. 163). Male genitalia with aedeagus with single V-shaped patch of sclerotized spinules; cerci with slender, curved, finger-like processes developed from basal article; supra-anal body membranous, hairy and weakly sclerotized (Fig. 95). Female subgenital plate emarginate; produced completely over sternum 9 and nearly all of sternum 10 (Fig. 98). A first

description of the mature nymph is given below.

Description. – Length from apex of head to end of abdomen in mature nymphs, 7.8 mm.

General color of head, thorax and abdomen pale brown; head and abdomen without conspicuous bands, spots or stripes of contrasting colors. Abdomen pale ventrally. Prothorax suboval, at least twice as long as broad, and dark brown on margin but may be lighter laterally. Mesothorax margined with dark brown at anterior end.

Wing pads with lateral margins broadly rounded.

Head with three ocelli forming nearly equilateral triangle; distance between ocelli about same as distance to inner margin of compound eye. Labium, maxillae and mandibles as Fig. 165–167. No occipital ridge.

Jewett (1955) figured the male genitalia, and Needham and Claassen (1925) and Gaufin *et al.* (1972) figured the female genitalia. Nymphal mouthparts are figured for the first time in Fig. 165–167.

Bionomics. – The biology of *Suwallia lineosa* is poorly known. In Battle Creek, adult emergence began early in July, 1975 and lasted at least three weeks. Several stages of maturity of nymphs from one sample were observed, indicating little synchrony of emergence. By the end of July nymphs were absent from benthic collections, suggesting a one-year life cycle since all had emerged.

Genus *Triznaka* Ricker

This genus was originally proposed as a subgenus of *Alloperla* (Ricker, 1952). Species of *Triznaka* have the male supra-anal process short and lying along the surface of and fused to the tenth tergum. It is usually in a slight depression but never in a deep groove. The tip of the process is directed upward and may be curved anterad, but there is no apparatus of erection (Fig. 94). Adults also have a black stripe on the abdominal terga, and a small anal lobe on the hindwing. Nymphal generic characters are not defined since few of the nymphs have been described.

Triznaka signata (Banks) (Fig. 94, 97, 159–162, 164, 185)

Chloroperla signata Banks 1895: 314.

Alloperla signata, Claassen 1940: 188.

Alloperla (Triznaka) signata, Ricker 1952: 186. – Gaufin 1964: 47. – Gaufin, Ricker, Miner, Milam and Hays 1972: 146.

Triznaka signata, Illies 1966: 154. – Baumann, Gaufin and Surdick 1977: 184.

Triznaka signata ranges from Washington and Montana south to Colorado and Utah. New collection records include Broad Creek and Mistohay Creek in northeastern Saskatchewan (Fig. 185).

Diagnostic Characters. – Average length, males 7.5 mm (from anterior margin of head to tip of folded wings); females, 9.8 mm. Adult head with anterior mark as long as broad and produced in midline to median ocellus in most specimens; ocellar triangle dark; pronotal rugosities only lightly pigmented; median pronotal mark broadly T-shaped, little produced laterally rearward (Fig. 164). Female subgenital plate extended over ninth sternum and broadly rounded posteriorly (Fig 97). A first description of the nymph is given below.

Description. – Length from apex of head to end of abdomen of mature nymphs, 8.0 mm.

General color of head, thorax and abdomen pale brown. Head with small light spot in front of anterior ocellus, and small light area at base of ocellar triangle extended posteriorly to end of head. Each compound eye connected to lateral ocelli by a light area. Prothorax suboval, at least twice as long

as wide with a lighter subcircular area in center, margin of dark brown, but broken laterally and at midline. Meso- and metathoracic regions patterned. Central median stripe on dorsal abdomen with two light spots on either side of stripe per segment. Abdomen pale ventrally; lateral margins of wing pads broadly rounded (Fig. 159).

Head with three ocelli forming a nearly equilateral triangle; distance between ocelli about same as distance to inner margin of compound eye. Labium, maxillae and mandibles as in Fig. 160–162. No occipital ridge.

Needham and Claassen (1925) and Gauvin *et al.* (1972) illustrated the male and female genitalia; first figures of the nymph are presented in Fig. 159–162.

Bionomics. – In Saskatchewan, mature nymphs were collected near the end of May and adults emerged in June of 1975 at Broad Creek. Nymphs of various stages of maturity could be collected in one sample indicating little synchrony of emergence. By July, nymphs were not present, indicating that all had emerged and a univoltine life history is probable.

Family Perlidae

Perlidae have profusely branched gills at lower angles of the thorax, the male epiproct reduced and inconspicuous and the Cu-A crossvein of the forewing located either in the anal cell or very close to it.

Both subfamilies of Perlidae, Acroneuriinae and Perlinae occur in Saskatchewan. The genital hooks of male acroneuriines are modified paraprocts. The subfamily occurs in the Americas and in southeastern Asia. Genital hooks of perlines are outgrowths of a cleft tenth tergum and paraprocts are little modified. This subfamily occurs in Africa, Eurasia and North America. Saskatchewan Perlidae, *Paragnetina media* and *Claassenia sabulosa* are in the subfamily Perlinae: *Acroneuria abnormis*, *Acroneuria lycorias*, *Hesperoperla pacifica* and *Perlesta placida* belong to the subfamily Acroneuriinae.

Genus *Paragnetina* Klapalek

Paragnetina members are characterized by the absence of anal gills, three ocelli, and a Y-shaped median ridge on the prosternum and mesosternum. Males are distinguished from those of other genera by having genital hooks arising from the side of the cleft tenth tergum and extending to the hind margin of the ninth tergum. The female subgenital plate is slightly produced past the hind margin of the eighth sternum (Fig 105). Nymphs have a transverse line of spinules on the occiput (Fig. 5). Five species of *Paragnetina* are presently known in North America and one occurs in Saskatchewan.

Paragnetina media (Walker) (Fig. 5, 105, 187)

Perla media Walker 1852: 145.

Acroneuria salvelini, Ricker 1935: 26.

Togoperla media, Claassen 1940: 150.

Paragnetina media, Ricker 1949: 287, and 1964: 59. – Harden and Mickel 1952: 51.

Paragnetina media occurs in the Maritimes to northern Ontario, central Quebec, Manitoba, northern Saskatchewan, northern Illinois, southern Michigan, central Pennsylvania and southern New England. A North American distribution map for the species was given by Ricker (1964) and the Saskatchewan distribution is illustrated in Fig. 187. Ricker (1944) reported the species from Wapus River in the Reindeer Lake region, and additional Saskatchewan collection localities include Mackay

Creek, Jct. Hwy. 2; Weyakwin River, Jct. Hwy. 2; Churchill River, Jct. Hwy. 2; stream 85 mi. N. of La Ronge, Sask., Jct. Hwy. 102; Bow River Jct. Hwy. 165; and Caribou Creek, Jct. Hwy. 106.

Diagnostic Characters. – Average length, males, 18 mm (from most anterior portion of head to tip of folded wings); females, 32 mm. Male fifth tergum produced very shallowly, broadly excavated or practically straight. Male genitalia with hooks rounded at tip; male sternum 9 without raised knob or “hammer”. Female subgenital plate little produced with base of median notch in line with sides of hind margin of sternum 8 (Fig. 105). Adult pronotum with black margins and black median stripe.

Nymphal abdominal terga uniformly brown, some specimens with faint median line (Fig. 5).

Needham and Claassen (1925), Frison (1935) and Hitchcock (1974) illustrated the adult genitalia; Claassen (1931) and Frison (1935) figured the nymph.

Bionomics. – Ricker (1949) noted that *Paragnetina media* was absent from colder trout streams and rivers of that region. Nymphs are usually found under stones in the larger streams but can also be collected in lakes and ponds (Claassen, 1931).

Though Claassen (1931) stated that nymphs of *Paragnetina media* probably require three years to complete their life cycle, Tarter and Krumholz (1971) found that in Kentucky *Paragnetina media* required only two years to complete the life cycle. In Saskatchewan, two size classes can be collected at one time, also suggesting a two year life cycle. For example, at Mackay Creek on June 5, 1974 seven mature nymphs with well-developed wing pads ranged from 20–23 mm in length (average length, 20.5 mm) and were near the end of their life cycle since the species emerged in the first week of July in both 1974 and 1975. Four specimens of the immature size class of nymphs, characterized by having poorly developed wing pads, ranged from 8.6–9.8 mm in length (average length, 9.5 mm). No very small nymphs were collected in mid-August and either the eggs from adults laid in July had not yet hatched or nymphs were yet too small to be collected in a sweep net. A significant growth of both hatchling nymphs and year-old nymphs must occur between fall and spring.

Harper and Pilon (1970) noted that the adult emergence period of *Paragnetina media* lasted from 5 to 25 days.

Based on dissected nymphs, the females produce an average of 802 eggs (Tarter and Krumholz, 1971) and the egg incubation period is 30 days at room temperature (Heiman and Knight, 1970).

Steffan (1965) described larvae of the new genus and species of Chironomidae (Diptera), *Plecopteracoluthus downesi*, which live phoretically on nymphal *Paragnetina media* in a gelatinous case and feed on detritus caught in the long hairs of the stonefly. Of the Perlidae carrying chironomids, six percent were *Paragnetina media*. In Saskatchewan, phoretic Chironomidae have not been found on *Paragnetina media* though they are commonly encountered on nymphs of *Acroneuria lyctorias*.

Adults of *Paragnetina media* are rarely encountered in the field. Sweeping the vegetation along stream banks and searching under rocks and under bridges yielded no specimens. This was also observed by Tarter and Krumholz (1971). The only adults examined in this study were from reared specimens. Females reared in laboratory aquarium cages where no males were present were found to produce egg masses even though copulation could not have occurred. Harper (1973a) incubated eggs laid by a virgin female and found that 13 percent hatched. This ability of eggs to develop parthenogenetically was thought to act as a safeguard in large carnivorous species, which are rarely abundant in their habitat, because the chances of meeting mates may be small. Frison (1935) noted that adults of *Paragnetina media* are diurnal and that mating occurs during the day.

Nymphs are carnivorous, feeding primarily on Ephemeroptera, Trichoptera and Diptera, but adults do not feed. Larvae are food for fish and crayfish (Tarter and Krumholz, 1971).

Genus *Claassenia* Wu

Males of *Claassenia* are distinct from other genera of Perlidae by having genital hooks darkly sclerotized at their tips and arising from lateral angles of tergum 10 (Fig. 8). Males also have a raised knob or "hammer" on sternum 9. The female subgenital plate is broadly rounded, usually with a shallow median recession and is little produced over sternum 9. It has with a row of spinules along its posterior margin (Fig 106). Nymphs resemble the eastern genus *Phasganophora* by having anal gills and an occipital ridge composed of closely set spinules, but are distinguished by having dorsal abdominal segments almost wholly brown and a banded pattern on the legs (Fig. 4).

Claassenia sabulosa, the single North American species of this genus, occurs in Saskatchewan.

Claassenia sabulosa (Banks)

(Fig. 4, 8, 106, 187)

Perla sabulosa Banks 1900: 242.

Claassenia languida, Needham and Claassen 1925: 100. – Claassen 1940: 181.

Claassenia arctica, Frison 1942a: 285.

Claassenia sabulosa, Ricker 1952: 190. – Jewett 1959: 90. – Gaufin, Ricker, Miner, Milam and Hays 1972: 156.

Claassenia sabulosa ranges from the cordilleran region of British Columbia and Alberta through the Cascade and Rocky Mountains to New Mexico and east to northern Manitoba and northern Ontario. Ricker (1964) provided a North American distribution map for the species. *Claassenia sabulosa* has not previously been reported from Saskatchewan, and new collection records include McDougal Creek, Jct. Hwy. 120; Creek at Mile 145, Jct. Hwy. 105; Overflowing River, Jct. Hwy. 109; Cluff Creek near Cluff Lake; and the South Saskatchewan River at the ferry N. of Lemsford, Sask. (Fig. 187). Though the species is abundant at McDougal Creek, it has rarely been collected in the South Saskatchewan River.

Diagnostic Characters. – Average length, brachypterous males, 19.6 mm (from anterior margin of head to end of abdomen); females, 31.4 mm (from anterior margin of head to wing tips). Since *Claassenia* is monotypic, generic characters also define specific characters.

Ricker (1938), Gaufin *et al.* (1966) and Gaufin *et al.* (1972) figured the adult genitalia; Claassen (1931) and Frison (1942a) figured the nymph.

Bionomics. – The habitat of *Claassenia sabulosa* is under stones in swift riffle areas where food is abundant (Richardson and Gaufin, 1971).

Three size classes of nymphs present in the same sample suggest a three-year life cycle. For example, on May 28, 1975 at McDougal Creek three nearly mature male nymphs with well developed wing pads averaged 23.0 mm and two females averaged 32.5 mm in length. Fourteen specimens in the next size class, with little wing pad development, averaged 13 mm in length and four specimens in the youngest age class, with no wing pad development, averaged 7.4 mm long. In 1975 adults emerged in the second week of July.

Richardson and Gaufin (1971) found that the species is carnivorous and Ephemeroptera make up the largest percentage of food ingested (37 per cent). Simuliid and chironomid larvae also comprised a large percentage of ingested material.

Frison (1942a) noted that the adults are nocturnal, emerging at nightfall and when active at dusk or night have the ability to move on the surface of the water somewhat like water-striders. Mating can take place as soon as a female emerges from its nymphal skin.

Genus *Acroneuria* Pictet

Sternal ridge patterns of nymphs and adult *Acroneuria* lack a distinct Y-shape, but three ocelli are present. Male *Acroneuria* have an undivided tenth tergum, paraprocts that are recurved into genital hooks and a hammer on the ninth sternum (Fig. 9, 102, 103). The female subgenital plate is little to moderately produced over the ninth sternum (Fig. 99, 100). Nymphs of most species lack an occipital ridge of closely set spinules, but if one is present it is broken at the midline. Seventeen species are known in North America; two occur in Saskatchewan.

Key to Saskatchewan species of *Acroneuria*

Adults

- 1 Remnants of subanal gills visible either dorsally or ventrally on tenth abdominal segment; head with ocellar triangle enclosed with dark brown to black sclerotization and extended anteriorly; female subgenital plate slightly emarginate (Fig. 100) *Acroneuria lycorias* (Newman), p. 50
- 1' No remnants of subanal gills; head with ocellar rings as only dark markings; female subgenital plate broadly rounded (Fig. 99) *Acroneuria abnormis* (Newman), p. 49

Nymphs

- 1 With subanal gills; general color dark brown and yellow dorsally (Fig. 2) *Acroneuria lycorias* (Newman), p. 50
- 1' Without subanal gills; general color light brown and yellow dorsally (Fig. 1) *Acroneuria abnormis* (Newman), p. 49

Acroneuria abnormis (Newman)
(Fig. 1, 99, 103, 186)

Perla abnormis Newman 1838: 177.

Acroneuria abnormis, Needham and Claassen 1925: 178. – Claassen 1940: 171. – Harden and Mickel 1952: 54. – Ricker 1964: 54. – Frison 1935: 391. – Hitchcock 1974: 149.

Acroneuria abnormis, a common prairie stonefly (Ricker, 1946), ranges from northern Quebec and the Maritimes to New England and south to Florida. It occurs west to Manitoba, Illinois and Minnesota. Stark and Gauvin (1976) reported *Acroneuria abnormis* from the South Saskatchewan River at Saskatoon, Sask., and additional collection localities include the North Saskatchewan River at Hwy. 5 (Borden Bridge), and 10 mi. E. of Prince Albert, Sask.; the South Saskatchewan River at the ferry N. of Lemsford, Sask.; and the Saskatchewan River 2 mi. S.W. of Nipawin, Sask. (Fig. 186).

Diagnostic Characters. – Average length, males, 25.0 mm (from anterior margin of head to tip of folded wings); females, 42.0 mm. Male genitalia with paraprocts broad, triangular and sharp; spinules present on terga 9 and 10 (Fig. 103). Female subgenital plate slightly produced and broadly rounded (Fig. 99).

Nymphs without anal gills; with light M-pattern in front of median ocellus (Fig. 1).

Needham and Claassen (1925) and Frison (1935) figured the adult genitalia and the nymph was illustrated by Claassen (1931) and Frison and Hitchcock (1974). Hitchcock (1974) noted that there was a wide range of variability in the abdominal color pattern of Connecticut nymphs, and a similar variation occurs in Saskatchewan specimens. It may vary from being all dark to having two broad, paired, semicircular dark patches on the basal part of most abdominal terga.

Bionomics. – Most nymphs of *Acroneuria abnormis* are found under larger rocks in water about one meter deep. Steffan (1967) noted that the species occurs in rivers where it is exposed to the strongest current.

The species probably has a three-year life cycle since three nymphal size classes can be collected at one time. For example, the average length of six near-mature nymphs with well-developed wing pads collected at the South Saskatchewan River (Lemsford Ferry) on May 23, 1974 was 25.5 mm. Six nymphs with little wing pad development averaged 17.6 mm in length, and two nymphs with no wing pad development averaged 8.2 mm long.

In Saskatchewan, adult emergence began in the first week of July of 1974 and 1975 and lasted approximately two weeks. Eggs evidently hatch soon after they are laid because a nymph measuring 2.66 mm long was collected at the ferry north of Lemsford, Sask. on August 9, 1974. The nymph would be the overwintering stage. Harper and Pilon (1970) graphed the emergence of the species in Quebec and suggested that emergence variation from year to year was dependent on water temperature. Males were found to emerge earlier than females. Hitchcock (1974) stated that nymphs are carnivorous and after a drought in which streams had dried up reported collecting small nymphs from the streams when they had again started to flow. Steffan (1967) observed that *Acroneuria abnormis* was active when the water temperature was -0.5 C, presumably in the absence of ice.

Steffan (1967) found that larval phoresis of a chironomid on *Acroneuria abnormis* was common in a Quebec stream. Eighty-three percent of chironomids on stonefly nymphs were on specimens of *Acroneuria abnormis*, evidently the preferred host. This type of phoresis is known for *Acroneuria lycorias* in Saskatchewan, but has not been observed for *Acroneuria abnormis*.

Acroneuria lycorias (Newman)
(Fig. 2, 100, 102, 186)

Perla lycorias Newman 1839: 35.

Acroneuria perbranchiata, Neave 1933: 236. – Claassen 1940: 175.

Acroneuria lycorias, Claassen 1940: 174. – Frison 1942a: 283. – Harden and Mickel 1952: 55. – Ricker 1964: 54. – Hitchcock 1974: 155.

Acroneuria lycorias occurs in northern Quebec and south through New England to Florida, and west to Ontario, Manitoba, Saskatchewan and Tennessee. It is common throughout its range. Cushing (1961) reported the species from Montreal River, and additional Saskatchewan collection records include (Fig. 186): Weyakwin River, Jct. Hwy. 2; stream 85 mi. N. of La Ronge, Sask., Jct. Hwy. 102; Mackay Creek, Jct. Hwy. 2; Nipekamew River, Jct. Hwy. 165; Jackfish Creek, Jct. Hwy. 8; Cub Creek, Jct. Hwy. 106; Nemeiben River, Jct. Hwy. 2; Torch River, Jct. Hwy. 106; Cole Creek, Jct. Hwy. 104; Puskwakau River, Jct. Hwy. 106; Arsenault River, Jct. Hwy. 104; Overflowing River, Jct. Hwy. 109; Red Deer River, Jct. Hwy. 23, and Jct. Hwy. 109; Pine Creek, Jct. Hwy. 165; Montreal River, Jct. Hwy. 2; Waterhen River, Jct. Hwy. 226; stream 87 mi. N. of Southend, Sask.; Ballantyne River, Jct. Hwy. 165; Churchill River, Jct. Hwy. 2, Pita Lake Rapids and Wapumon Lake Rapids; Caribou Creek near Caribou Lake, Jct. Hwy. 106; Bear River, Jct. Hwy. 106; Martineau River, Jct. Hwy. 55; Little Red River, near Prince Albert, Sask.; Bow River, Jct. Hwy. 165; Waskesiu River, Jct. Hwy. 2; and Beaver River, Jct. Hwy. 155.

Diagnostic Characters. – Average length, males, 18.0 mm (from anterior margin of head to tip of folded wings); females, 35.0 mm. Male genitalia with paraprocts flattened, triangular and sharply pointed at anteriorly directed tips; spinules present on terga 9 and 10 (Fig. 102). Female subgenital plate produced and flattened or emarginate apically (Fig. 100). Adult head with ocellar triangle dark. Adult

with anal gill remnants.

Nymphs with anal gills; banded pattern on abdominal terga; light M-pattern in front of anterior ocellus (Fig. 2).

Needham and Claassen (1925), Hitchcock (1974) and Frison (1942a) figured the adult genitalia, and Frison (1942a) illustrated the nymph.

Bionomics. – In Saskatchewan, *Acroneuria lycorias* seems to have a three-year life cycle since three size classes of nymphs can be collected at one time. For example, at the Nemeiben River on June 5, 1974, the average length of seven mature nymphs with well-developed wing pads was 25.3 mm; the average length of five immature nymphs which had little wing pad development was 20.0 mm, and the average size of six very immature nymphs with no wing pad development was 10.1 mm.

In Saskatchewan, emergence occurs about the first two weeks of July. Harper and Pilon (1970) noted that the emergence period is short.

Nymphs have most often been collected from under rocks in rapids, and are probably carnivorous.

Steffan (1967) noted that chironomid larvae of *Plecopteracoluthus downesi* were phoretic on nymphs of *Acroneuria lycorias*. Of the Perlidae carrying chironomid larvae, three per cent were *Acroneuria lycorias*. In Saskatchewan, phoresis of a chironomid on *Acroneuria lycorias* nymphs is very common in some rivers.

Genus *Hesperoperla* Banks

In *Hesperoperla* male paraprocts are flattened, triangular and pointed; spinules are absent from both the ninth and tenth abdominal terga (Fig. 101). The female subgenital plate is produced over half of sternum 9; the hind margin is slightly angulate and usually has squarish shiny spot at its apex (Fig. 104). The nymph has anal gills but lacks an occipital ridge. The nymphal head has a yellow mark extending from labrum to the anterior ocellus, and the abdominal terga are brown (Fig. 3).

Hesperoperla, a monotypic genus, occurs in Saskatchewan.

Hesperoperla pacifica (Banks)

(Fig. 101, 104, 186)

Acroneuria pacifica Banks 1900: 242. – Frison 1942b: 72. – Jewett, S.G. 1959: 89. – Claassen 1940: 175. *Acroneuria pumila*, Banks 1906: 335.

Acroneuria okanagan, Ricker 1935: 262. – Claassen 1940: 173.

Acroneuria (Hesperoperla) pacifica, Ricker 1943: 130. – Gaufin, Ricker, Miner, Milam and Hays 1972: 154.

Hesperoperla pacifica, Illies 1966: 336. – Baumann, Gaufin and Surdick 1977: 162.

Hesperoperla pacifica ranges from British Columbia to California and New Mexico and east to Alberta and South Dakota. This first Saskatchewan collection record is from Cypress Hills at Battle Creek near Reesor Lake (Fig. 186). It was abundant at this locality but was not collected further downstream in the same river near Consul, Sask.

Diagnostic Characters. – Average length, males, 25 mm (from anterior margin of head to tips of folded wings); females, 37 mm. Since this is the only known species of *Hesperoperla*, generic characters also define specific characters.

Needham and Claassen (1925), Gaufin *et al.* (1972), Stark and Gaufin (1966) figured the adult genitalia; Claassen (1931) figured the nymph.

Bionomics. – Three size classes of nymphs have been collected at one sampling time suggesting a three-year life cycle. For example, four near-mature nymphs with well-developed wing pads were collected at Battle Creek on June 3, 1975 which averaged 28.5 mm long. Nineteen nymphs with little wing pad development averaged 14.9 mm long and seven very immature nymphs with no wing pad development averaged 5.3 mm long.

In 1975 adults emerged about the last week of June and emergence lasted for approximately two weeks.

Richardson and Gaufin (1971) found the species to be carnivorous, its diet consisting of 88.3 per cent animal matter. The prey was chiefly Ephemeroptera nymphs and chironomid and Trichoptera larvae.

Genus *Perlesta* Banks

Adults of this genus have remnants of nymphal subanal gills, a yellowish-white costal margin in the forewings, and lack anal crossveins. Males have spinule patches only on the tenth abdominal tergum and lack a hammer on sternum 9. Paraprocts are sclerotized and recurved over the tenth tergum. The female subgenital plate is slightly produced, and distinctly notched mesally. Nymphs have a distinct occipital ridge and dark freckled spots on abdominal terga.

Superficially, *Perlesta* adults resemble *Isoperla* but the gill remnants and light coloring in the costal area of the wing are distinctive.

Two species are presently recognized in North America and one occurs in Saskatchewan.

Perlesta placida (Hagen) (Fig. 187)

Perla placida Hagen 1861: 28.

Perlesta placida, Needham and Claassen 1925: 158. – Frison 1942a: 271. – Ricker 1964: 54. – Hitchcock 1974: 161.

Perlesta placida is a widely distributed species occurring from the Maritimes to Florida and west to Manitoba, Wyoming and Texas. This first Saskatchewan record is the most northerly range extension of the species. It has been collected from Bisset Creek, Jct. Hwy. 55, and from the Assiniboine River near Tadmore, Sask., Jct. Hwy. 9 (Fig. 187).

Diagnostic Characters. – Average length, males, 8.5 mm (from anterior margin of head to tip of folded wings); females, 14 mm. Adult head with central, longitudinal black stripe darkest between ocelli. Male genitalia with genital hooks tapered from bases to tips. Female subgenital plate slightly produced, notched in center, and covered with long hairs.

Nymphs with speckled appearance; with single light stripe extended down midline of abdomen; abdominal terga lined with intercalary spinules.

Needham and Claassen (1925), Frison (1935, 1942a), and Hitchcock (1974) figured the adults; Claassen (1931) and Frison (1935) figured the nymph.

Bionomics. – Stewart *et al.* (1969) studied the mating behaviour of *Perlesta placida*. Males lived four to six days and females lived seven to eight days; both could mate several times during this period. Mating occurred the first day after adult emergence and began by the aggressive capture of females by the males soon after contact. The male genital hooks attached to the lobes of the female subgenital plate allowing a space between the male subanal lobes directly below the female genital opening. This space served as a "channel" for the aedeagus which was everted from beneath the posterior portion of the

subgenital plate, through the space, and into the female genital opening.

This species has been found in a wide variety of streams, even intermittent ones (Harden and Mickel, 1952). In Saskatchewan, it emerges in mid-summer: mature nymphs were collected at Bisset Creek on July 19, 1976; adults were found on July 22, 1976. Nymphs are carnivorous, feeding mainly on chironomid larvae (Frison, 1935).

Family Perlodidae

Although few features characterize this family as a whole, perlodids all have slender maxillary palpi and glossae reduced to small knobs fused to the side of the paraglossae. Perlodidae differ from Perlidae by the absence of dissected thoracic gills, and pointed rather than rounded paraglossae. Although a few exceptions occur, perlodids are distinct from chloroperlids by having the two branches of A_2 in the forewing leaving the anal cell separately and by having a flatter nymphal body.

This family occurs in North America, Eurasia and northern Africa and has been divided into three subfamilies: the more primitive Isogeninae, and more highly advanced Perlodinae and Isoperlinae. Isogninae have a cleft male tenth tergum, a well developed supra-anal process, and usually have submental gills. Male paraprocts are generally produced into recurved hooks in Isoperlinae and project upward or backward in Perlodinae. All three subfamilies are represented in Saskatchewan. *Isogenoides*, *Arcynopteryx* and *Skwala* are in the subfamily Isogninae; *Isoperla* belongs to Isoperlinae and *Diura* is a representative of Perlodinae.

Genus *Arcynopteryx* Klapálek

Arcynopteryx is characterized by having a mesosternal Y-ridge attached to the anterior corners of the furcal pits and the absence of a transverse ridge (Fig. 25). The male ninth tergum is emarginate and bears many spinules on its posterior margin. The tenth tergum is cleft with the posterior section modified into a pair of flat arms on dorsal lobes which are curved in a lateral direction. The supra-anal process consists of a very long, thin spine projecting from an expansive membranous region (Fig. 113). The female subgenital plate is broad, produced halfway or more over sternum 9, and is trilobed or occasionally bilobed (Fig. 115). Nymphs lack abdominal and thoracic gills but have well-developed submental gills. Nymphal mandibles usually lack denticles on their cusps but may have a few present on the outer left cusp only. The major cusp of these mandibles is slightly serrate marginally.

This Holarctic genus is monotypic and occurs in Saskatchewan.

Arcynopteryx compacta (MacLachlan) (Fig. 113, 115, 188)

Dictyopteryx compacta MacLachlan 1872: 53.

Arcynopteryx lineata, Smith 1917: 476.

Arcynopteryx ignota, Smith 1917: 479.

Arcynopteryx inornata, Smith 1917: 480.

Perlodes minor, Ricker 1938: 144.

Arcynopteryx minor, Hanson 1942: 396

Arcynopteryx americana, Ricker 1943: 114, and 1944: 183.

Arcynopteryx compacta, Brinck 1949: 58. – Illies 1966: 352.

In North America, *Arcynopteryx compacta* extends from the arctic southward to Colorado, Lake Superior and New Hampshire. The single Saskatchewan record was given by Ricker (1944) from Tazin River near Lake Athabasca. Ricker (1964) presented a North American distribution map of the species; the Saskatchewan collection record is mapped in Fig. 188.

Diagnostic Characters. – Average length, brachypterous males, 11 mm (from anterior margin of head to end of abdomen); females, 20 mm. (from anterior part of head to tip of folded wings). Since this is the only known species of *Arcynopteryx*, generic characters also define specific characters.

Hanson (1942) figured the male and female genitalia; Brinck (1949) figured the nymph.

Bionomics. – Brinck (1949) found that adults of *Arcynopteryx compacta* emerge in mid-summer during the night or early morning when humidity is highest. After mating, the female carries the extruded egg mass on the abdomen and the eggs fall off as the female runs across the water. The eggs then become attached to the substrate by adhesive projections. Nymphal growth is greatest in fall and the following spring. Nymphs are mainly carnivorous feeding on mayfly and chironomid larvae.

Genus *Skwala* Ricker

This genus has the arms of the mesosternal Y-ridge terminating at the anterior corners of the furcal pits; a transverse ridge is absent. The male tenth tergum is cleft with inward and forward directed lobes which are fairly long and spinulose. The male lateral stylets are well-developed (Fig. 112). The female subgenital plate is produced somewhat and truncate (Fig. 114). The nymphal mandibles have numerous denticles along both sides of their outer cusps (Fig. 28).

This genus is represented by two North American species; one occurs in Saskatchewan.

Skwala parallela (Frison) (Fig. 25, 28, 35, 112, 114, 177)

Perlodes americana, Needham and Claassen 1925: 61. – Claassen 1940: 111.

Hydroperla parallela, Frison 1936: 261, and 1942a: 298. – Claassen 1940: 104.

Arcynopteryx (Skwala) parallela, Ricker 1943: 113. – Jewett 1959: 64.

Skwala parallela, Illies 1966: 378.

Skwala parallela has been previously reported from western Canada and United States, including British Columbia, Oregon, California and Utah. In Saskatchewan it occurs in the following localities (Fig. 188): McDougal Creek, Jct. Hwy. 120; Cub Creek, Jct. Hwy. 106; Mackenzie Creek, Jct. Hwy. 165; Shuard Creek, 11 mi. S. of Piapot, Sask.; and Battle Creek, Cypress Hills, near Reesor Lake.

Diagnostic Characters. – Average length, brachypterous males, 19.0 mm (from anterior margin of head to end of abdomen); females, 25.0 mm (from anterior margin of head to tip of folded wings). Male genitalia with tenth tergum cleft; subcylindrical lobes medially on tergum 10, 2–3 times as long as breadth of their middle constricted portion (Fig. 112). Female subgenital plate extended only slightly over sternum 9; posterior margin straight and corners angulate (Fig. 114).

Nymphs with serrations along major mandibular cusps (Fig. 28); partial occipital ridge, interrupted in middle, borders hind margins of compound eyes.

Frison (1936, 1937) and Gauvin *et al.* (1972) figured the male and female genitalia; Frison (1942a) figured the nymph.

Bionomics. – Mature nymphs of *Skwala parallela* were collected from Battle Creek near Reesor Lake on March 28, 1976 and from Cub Creek, Jct. Hwy. 106 and McDougal Creek, Jct. Hwy. 120 on April 12, 1976. Adults were collected from Battle Creek (Reesor Lake) on May 19, 1976.

Richardson and Gaufin (1971) found that nymphs lived beneath rocks in swift, well-oxygenated water and were principally carnivorous, feeding on mayfly and chironomid nymphs, and occasionally on small stonefly nymphs. Filamentous algae, diatoms and detritus also formed significant parts of the diet.

Genus *Diura* Billberg

Diura, the only North American Perlodinae, is characterized by having an uncleft male tenth tergum and paraprocts which are extended backward to meet on the median margin of the tenth tergum (Fig. 107). Females have the subgenital plate produced halfway or more over the ninth sternum (Fig. 108, 109). Nymphs have dark abdominal terga with large paired spots laterally and a few smaller lateral spots. The nymphal lacinia, or inner projecting process of the maxilla, has a sharp angle just below the smaller tooth (Fig. 10) in contrast to other Saskatchewan perlodid genera in which the region below the smaller tooth is rounded or, more commonly, tapering from the tooth to the base (Fig. 170).

This genus is represented by three species in North America: two are Holarctic (*nanseni* and *bicaudata*) and one (*knowltoni*) occurs in western United States and Canada. *Diura bicaudata* occurs in northern Saskatchewan.

Diura bicaudata (Linnaeus)

Phryganea bicaudata Linnaeus 1758: 548.

Dictyopterygella postica, Ricker 1944: 178.

Diura bicaudata, Brinck 1949: 61.

This Holarctic species has North American reports from Alaska, Yukon, Mackenzie, and Keewatin. This first Saskatchewan record is based on a collection of a single female nymph from the shore of Wollaston Lake (Fig. 189) by D.S. Rawson and identified by W.E. Ricker.

Diagnostic Characters. – Average length, brachypterous males, 12.0 mm (from anterior margin of head to end of abdomen); females, 17.0 mm (from anterior margin of head to tip of folded wings). Male genitalia with subanal lobes produced posterad, together subcylindrical, and glabrous with tips lighter than the remainder (Fig. 107). Female subgenital plate variable. Ricker (1944) reported specimens with subgenital plate produced about halfway over sternum 9, its sides broadly rounded and deeply excavated. Brinck (1949) presented figures showing eight different forms of subgenital plate. Drawings presented here (Fig. 108, 109) show two common forms of subgenital plate with posterior edge broadly rounded (Fig. 108), and shallowly emarginate medially (Fig. 109).

Nymphs without underlying adult characters are presently indistinguishable from other species of *Diura*.

Bionomics. – Brinck (1949) has reported females of *Diura bicaudata* ovipositing while walking across the water surface or when flying. Egg incubation was found to last one to two months with nymphs showing a high growth rate in autumn and spring, but very retarded winter growth.

Nymphs are mainly predatory, feeding on chironomid larvae but occasionally they ingest vegetable matter (Brinck 1949).

Genus *Isogenoides* Klapalek

Isogenoides, the only Saskatchewan representative of Isogeninae, is characterized by having the arms of the mesosternal Y-ridge meeting the posterior corners of the furcal pits in addition to having a

median ridge joining the transverse ridge to the fork of the Y (Fig. 24). Submental gills are long. The male tenth tergum is completely cleft, and the genital lobes are directed medially or anteriorly rather than posteriorly. The male supra-anal process is slender with a terminal or subterminal hook or hooks. Lateral stylets are slender, acute or blunt, and the subanal lobes are quite expanded (Fig. 110, 111). The female subgenital plate is moderately produced, and either rounded or notched (Fig. 116). Nymphal mandibles usually have the ventral cusps serrate marginally but the denticles are minute.

Two of nine North American species of *Isogenoides* occur in Saskatchewan. These are the closely related species *Isogenoides colubrinus* (Hagen) and *Isogenoides frontalis* (Newman) which were ranked as subspecies of *Isogenoides frontalis* by Ricker (1952) but assigned full specific status by Illies (1966). *Isogenoides colubrinus* and *Isogenoides frontalis* are separable taxonomically only by examination of the male genital structures; Ricker (1952) was unable to establish characters to distinguish between females. I have reared a large series of females of both species but also have been unable to find any differences between the two which hold true for all or even most specimens. Nymphs of the two species have shown a similar agreement in all characters examined.

Key to Saskatchewan species of *Isogenoides*

Males

- 1 Posterior inner angles of genital hooks (terminal sclerotized corners of 10th tergum) sharp, practically a right angle (Fig. 110)..... *Isogenoides colubrinus* (Hagen), p. 56
- 1' Posterior inner angles of the genital hooks broadly obtuse or rounded (Fig. 111) *Isogenoides frontalis* (Newman), p. 57

Isogenoides colubrinus (Hagen)
(Fig. 20, 24, 38, 110, 116, 189)

Isogenus colubrinus Hagen 1874: 576. –(in part) Claassen 1940: 106. – Ricker 1964: 55, 67.
Isogenoides frontalis, Hanson 1943: 660.
Isogenus frontalis, Harden and Mickel 1952: 33.
Isogenus (Isogenoides) frontalis colubrinus, Ricker 1952: 110.
Isogenoides colubrinus, Illies 1966: 363.

Isogenoides colubrinus is known in Alaska, the cordilleras to Utah, northern Alberta to the Mackenzie River, Great Slave Lake, Lake Athabasca, central Saskatchewan and as far east as The Pas, Manitoba. Ricker (1946) reported the species from St. Laurent, Sask. (South Saskatchewan River) and additional collection records (Fig. 189) include the North Saskatchewan River, Jct. Hwy. 5 (Borden Bridge); South Saskatchewan River at the ferry north of Lemsford, Sask., the ferry Fenton, Sask., and the ferry north of Birch Hills, Sask.; and the Saskatchewan River 2 mi. S.W. of Nipawin, Sask. Ricker (1964) mapped the North American distribution pattern of this species.

Diagnostic Characters. – Average length, males, 18.0 mm (from anterior part of head to tip of folded wings); females, 24.0 mm. Adults with submental gills long; fork of the mesosternal Y-ridge connected with transverse ridge (Fig. 24). Male genitalia with posterior angles of genital hooks slightly acute and approaching right angles (Fig. 110); epiproct with hook at its tip. Female subgenital plate only slightly produced with deep U-shaped notch (Fig. 116).

Nymphal mandibles in most specimens serrate marginally, with scarcely distinguishable denticles; abdominal terga uniformly light brown.

Hanson (1943) and Gaufin *et al.* (1972) figured the male and female genitalia; Claassen (1931)

figured the nymph.

Bionomics. – In Saskatchewan, mature nymphs were collected from Lemsford Ferry, Borden Bridge, and Birch Hills Ferry in mid-May of 1974 and 1975. Adults were collected at the end of May of 1974. Mature nymphs were not found in collections from the North and South Saskatchewan Rivers from mid-June onward in both 1974 and 1975 with the unusual exception of two mature nymphs from Lemsford Ferry on July 7, 1975. They were reared and emerged in the laboratory on July 10, 1975. Eggs apparently develop rapidly since six immature nymphs averaging 5 mm in length were collected from Lemsford Ferry on August 10, 1974.

Isogenoides frontalis (Newman)
(Fig. 111, 189)

Isogenus frontalis Newman 1838: 178. – (in part) Claassen 1940: 106. – Frison 1942a: 290. – Ricker 1964: 65, 67.

Isogenus hudsonicus, Hanson 1943: 662.

Isogenus (Isogenoides) frontalis frontalis, Ricker 1952: 110.

Isogenoides frontalis, Illies 1966: 365.

Isogenoides frontalis is considered an eastern and northern species (Ricker, 1952) ranging from the Maritimes to northeastern United States and west to Michigan, Minnesota and Churchill, Manitoba. This first Saskatchewan report represents the most westerly range extension of the species. Specimens have been collected from the following localities (Fig. 189): Weyakwin River, Jct. Hwy. 2; stream at mile 83, Jct. Hwy. 106; stream at mile 85, Jct. Hwy. 102; stream 39 mi. N. of Hudson Bay, Sask., Jct. Hwy. 109; Meeyomoot River, Jct. Hwy. 165; Torch River, Jct. Hwy. 106; Waskwei River, Jct. Hwy. 109; Puskwakau River, Jct. Hwy. 106; and Mistohay Creek, Jct. Hwy. 226.

Ricker (1964) presented a North American distribution map of this species. The species is probably much more widespread than indicated on the Saskatchewan distribution map since I have collected nymphs and females from several other northern rivers which key to *Isogenoides*, but without adult males it is impossible to assign specific names to these specimens. I believe them to be *Isogenoides frontalis* since *Isogenoides colubrinus* has been found only in the Saskatchewan River System.

Diagnostic Characters. – *Isogenoides frontalis* differs from *Isogenoides colubrinus* only in shape of male genital hooks. In *Isogenoides frontalis*, posterior inner angles of genital hooks are broadly obtuse or rounded (Fig. 111).

Needham and Claassen (1925), Frison (1942a) and Hanson (1943) figured the male and female genitalia; Frison (1942a) figured the nymph.

Bionomics. – *Isogenoides frontalis* appears to have a one-year life cycle. Forty-three mature nymphs with well-developed wing pads collected from Weyakwin River, Jct. Hwy. 2 on May 6, 1976 had an average length of 20.2 mm. There were no nymphs of a younger age-class present (less than 17 mm in length). Adult emergence occurred at the end of May and early June of 1974 and 1975. Nymphs were absent from samples taken from the same river in late June and mid-July of 1974 and 1975. Egg development and early nymphal growth appear rapid since twelve early-instar nymphs averaging 8.9 mm in length were collected from Weyakwin River on August 8, 1975.

Genus *Isoperla* Banks

Males of this genus are characterized by having an uncleft tenth tergum, the absence of both gills and epiproct, and modified paraprocts. The male eighth sternum bears a lobe on its hind margin

(except in *maxana* Harden and Mickel which has lobes on both sterna 7 and 8 and in *ebria* (Hagen) and *trictura* (Hoppe) in which lobes are absent). Females of *Isoperla* are difficult to separate from *Isogenoides*, but in most *Isoperla* species females do not have subgenital plates produced as greatly as in *Isogenoides*. Most nymphs have a longitudinal or transverse striped pattern on the abdomen.

This large, difficult genus is in great need of revision; many of the 50 known species probably should be synonymized.

Because there is a great variation in both color patterns and genitalic structures within many species, the keys, taken largely from Frison (1942a), Gaufin *et al.* (1972) and Hitchcock (1974) may be inoperative for some specimens.

Key to Saskatchewan species of *Isoperla*

Adults

- 1 Ninth ventral abdominal segment much produced posteriorly and recurved upward, sternum 10 mostly or entirely concealed. Sternum 8 with small lobe in middle of posterior portion (Fig. 118)(males) 2
- 1' Ninth ventral abdominal segment poorly or not at all produced; tenth segment always visible from below. Sternum 8 without small lobe in middle of posterior portion; posterior margin either broadly rounded or strongly produced as subgenital plate (females)..... 8
- 2 (1) Cerci about twice as long as relaxed abdomen, length of 12th cercal article 6 to 8 times its greatest width; two conspicuous semi-circular patches of spinules on ninth abdominal tergum (Fig. 120)..... *Isoperla longiseta* Banks, p. 61
- 2' Cerci less than 1.5 times as long as relaxed abdomen, length of 12th cercal article 3 to 5 times its greatest width; if spinules present on abdominal tergum 9, spinules not arranged in semi-circular pattern 3
- 3 (2') Patches of short stout hairs on posterior margin of tergum 9; most specimens with red tinge to some abdominal segments (Fig. 122) *Isoperla patricia* Frison, p. 62
- 3' No patches of stout hairs on tergum 9; most specimens without red tinge to abdominal segments..... 4
- 4 (3') Longitudinal dark stripes on abdominal terga (Fig. 119)..... *Isoperla transmarina* (Newman), p. 64
- 4' Abdomen uniformly brown or yellow 5
- 5 (4') Paraprocts projecting little if at all over tergum 10 (Fig. 117, 118, 121) 6
- 5' Paraprocts recurved upward and forward over tergum 10 (Fig. 123)..... 7
- 6 (5) Paraprocts scarcely sclerotized (Fig. 117, 118)..... *Isoperla bilineata* (Say), p. 60
- 6' Paraprocts very heavily sclerotized (Fig. 121)..... *Isoperla decolorata* (Walker), p. 60
- 7 (5') Aedeagus with slender process, forked at its base and visible as rod-shaped structure through sternum 9 (Fig. 123, 124) *Isoperla petersoni* Needham and Christensen, p. 63
- 7' Aedeagus without slender sharp process *Isoperla marlynia* Needham and Claassen, p. 62
- 8 (1') Light spot in ocellar triangle broadly open caudally, forming a broad V; subgenital plate subtriangular or slightly notched posteriorly (Fig. 125-128)..... *Isoperla bilineata* (Say), p. 60
- 8' Ocellar triangle completely enclosed by dark sclerotization with central light spot completely enclosed or narrowly open caudally; subgenital plate variable 9
- 9 (8') Cerci about twice as long as relaxed abdomen, length of 12th cercal article 6 to 8 times

	its greatest width; subgenital plate rounded in most specimens, slightly excavated, or rarely slightly pointed (Fig. 129–132)	<i>Isoperla longiseta</i> Banks, p.	61
9'	Cerci less than 1.5 times as long as relaxed abdomen, length of the 12th cercal article 3 to 5 times its greatest width; subgenital plates variable		10
10 (9')	Subgenital plate truncate (Fig. 135)	<i>Isoperla transmarina</i> (Newman), p.	64
10'	Subgenital plate not truncate		11
11 (10')	Subgenital plate subtriangular (Fig. 133)	<i>Isoperla decolorata</i> (Walker), p.	60
11'	Subgenital plate not subtriangular		12
12 (11')	Subgenital plate with deep wide excavation (Fig. 136); most specimens with red cast to some abdominal segments	<i>Isoperla patricia</i> Frison, p.	62
12'	Subgenital plate without deep, wide excavation; without red tinge to abdominal segments.....		13
13 (12')	Species with lateral light spots anterior to median ocellus and with crescent-shaped light spot anterior to median ocellus (Fig. 137).....	<i>Isoperla marlynia</i> Needham and Claassen, p.	62
13'	Species without lateral light spots anterior to median ocellus and without subcircular light spot anterior to median ocellus (Fig. 134)	<i>Isoperla petersoni</i> Needham and Christensen, p.	63
Nymphs			
1	Abdominal terga with longitudinal stripes		2
1'	Abdominal terga with transverse stripes with both posterior and anterior tergal margins dark and middle tergal portion light	<i>Isoperla marlynia</i> Needham and Claassen, p.	62
2 (1)	Abdominal stripes indistinct; 6 to 8 dark dots on each abdominal terga	<i>Isoperla bilineata</i> (Say), p.	60
2'	Abdominal stripes distinct, no dark dots on abdominal terga		3
3	Cerci less than 1.5 times as long as relaxed abdomen		4
4 (3')	Abdominal terga with broad longitudinal yellow band in center bordered on each side by dark band	<i>Isoperla petersoni</i> Needham and Christensen, p.	63
4'	Abdominal terga with narrow dark band in center bordered on either side by light band.....		5
5 (4')	Light spot within ocellar triangle very small and inconspicuous (Fig. 168).....	<i>Isoperla decolorata</i> (Walker), p.	60
5'	Light spot within ocellar triangle at least as large in diameter as half the distance between lateral ocelli		6
6 (5')	Abdominal terga with central dark band bordered on each side by a much broader light band; light area within ocellar triangle equal in diameter to about half the distance between lateral ocelli	<i>Isoperla patricia</i> Frison, p.	62
6'	Abdominal terga with central dark band bordered on each side by light band of about the same width; light area within ocellar triangle equal in diameter to more than half the distance between lateral ocelli	<i>Isoperla transmarina</i> (Newman), p.	64

Isoperla bilineata (Say)
(Fig. 31, 117, 118, 125-128, 190)

Sialis bilineata Say 1823: 165.

Isoperla bilineata, Needham and Claassen 1925: 154. – Frison 1935: 436. – Claassen 1940: 198. – Harden and Mickel 1952: 39. – Ricker 1964: 54.

Isoperla bilineata is a common species from central and eastern Canada and the United States. It has been collected from Newfoundland, New York, New Jersey and North Carolina and west to Saskatchewan, Minnesota and Colorado. Needham and Claassen (1925) reported the species from "Saskatchewan", and additional collection records (Fig. 190) include: Little Red River near Prince Albert, Sask.; the North Saskatchewan River at Hwy. 5 (Borden Bridge), Hwy. 12, Prince Albert, Sask., Cecil Ferry, and the ferry north of Maidstone, Sask.; the South Saskatchewan River at Saskatoon, Sask., Fenton Ferry, ferry north of Lemsford, Sask., ferry east of Hague, Sask., ferry north of Birch Hills, Sask.; Battle River, 4 mi. S. of Lashburn, Sask.; Fox Creek; and the river 87 mi. N. of Southend, Sask. on the Wollaston Lake Road.

Diagnostic Characters. – Average length, males, 10.0 mm (from anterior margin of head to tip of folded wings); females, 14.0 mm. Adults with head and body pale in color; ocelli in most specimens connected by dark V-shaped mark. Male genitalia with paraprocts little modified, scarcely sclerotized and somewhat recurved; lobe on sternum 8 broadly rounded (Fig. 117, 118). Female subgenital plate sub-triangular and produced about halfway over sternum 9 (Fig. 126); or is slightly emarginate posteriorly (Fig. 127, 128).

Nymphs with dark longitudinal stripes and six to eight dark dots on abdominal terga and light spot in ocellar triangle.

Needham and Claassen (1925) and Frison (1935) figured the adult genitalia and wings; Frison (1935) and Claassen (1931) figured the nymph.

Bionomics. – Frison (1935) noted that *Isoperla bilineata* was a member of the Illinois spring stonefly fauna with adult emergence occurring at night and beginning by the end of March. Maximum abundance of adults was reached in mid-May and adults were absent by the end of June. In Saskatchewan, adults first appear by the end of May, and the species is very commonly collected throughout June but practically absent by July. One peculiar collection was a female from the stream 87 mi. N. of Southend, Sask. on the Wollaston Lake Road on August 7, 1975. This record is interesting because of the late collection date and northern location.

There is some confusion regarding the feeding habits of this species. Frison (1935) stated that the species seemed to be herbivorous, but Harden and Mickel (1952) found the larval gut contents to be principally Chironomidae. Eggs collected in June and kept in the laboratory did not hatch until October (Harden and Mickel, 1952).

Isoperla decolorata (Walker)
(Fig. 121, 133, 168-170, 192)

Perla decolorata Walker 1852: 170.

Isoperla decolorata, Claassen 1940: 199. – Ricker 1944: 183. – Ricker, 1955: 256. – Ricker 1964: 56.

Isoperla decolorata is a rare species known only from northern Canada (Great Bear Lake, Keewatin, Fort Churchill, northern Ontario) and Alaska. The collection of a single male from the North Saskatchewan River at Hwy. 5 (Borden Bridge) represents the most southerly known locality for this species.

Diagnostic Characters. – Average length, males, 10.5 mm (from anterior margin of head to tip of wings); females, 11.5 mm. Adults with general dark brown color and yellow markings; ocellar spot small and inconspicuous. Male sternum 8 with lobe broad at tip and constricted at base. Male genitalia with darkly sclerotized paraprocts fairly broad at their bases, sharp at tips and recurved but not over tergum 10 (Fig. 121). Female subgenital plate subtriangular with broad base extended about halfway over sternum 9 (Fig. 113). A first description of the nymph is given below.

Description. – Total length of mature nymph about 10 mm.

General color yellow with fuscous areas on head, thorax and abdomen as in Fig. 168; light yellow ventrally. Antennae light brown with first two articles darker; legs light yellow and darker at joints; cerci light brown.

Head with ocelli forming nearly equilateral triangle; maxillae and mandibles as in Fig. 169, 170.

Abdominal terga with central longitudinal dark stripe and light subcircular areas on either side; tergum 10 with central bilobed light area, as in Fig. 168. Abdominal terga covered with numerous clothing hairs and longer bristles on posterior margins of each terga, longest about one-third the mid-dorsal tergal length. Cerci with regular whorls of bristles near anterior margin of each article and a few long hairs which become more numerous on distal cercal articles.

Ricker (1944) figured the male and female genitalia; the nymph is illustrated for the first time in Fig. 168–170.

Bionomics. – Little is known of the biology of this species. From a sample of 205 *Isoperla* collected and reared from the North Saskatchewan River at Hwy. 5 (Borden Bridge) on May 27, 1975 only one was *Isoperla decolorata*; the remainder were *Isoperla bilineata*. The *Isoperla decolorata* adult emerged May 29, 1975 in the laboratory.

Isoperla longiseta Banks
(Fig. 120, 129–132, 191)

Isoperla longiseta Banks 1906: 337. – Needham and Claassen 1925: 156. – Claassen 1940: 203. – Frison 1942a: 318. – Ricker 1943: 124. – Harden and Mickel 1952: 41. – Ricker 1964: 56.

Isoperla longiseta is considered a typical prairie species (Ricker, 1964) and is abundant in large rivers of the plains and inter-mountain regions from the Mississippi to the Great Basin and from Colorado and Missouri northward. In Canada it occurs characteristically on the prairies but also as far north as Norman Wells on the Mackenzie River. Ricker (1946) reported several collections of this species from Saskatoon, Sask., and additional records (Fig. 191) include: the North Saskatchewan River at Hwy. 5 (Borden Bridge), North Battleford, Sask., Cecil Ferry, ferry south of Maymont, Sask., Prince Alberta, Sask., and the ferry 20 mi. N. of Lloydminster, Sask.; the South Saskatchewan River at the ferry north of Lemsford, Sask., the ferry north of Birch Hills, Sask., and the ferry north of Fenton, Sask.; the Saskatchewan River 2 mi. S.W. of Nipawin, Sask., and 10 mi. E. of the Squaw Rapids Power Station; and a record from Melfort, Sask.

Ricker (1964) presented a North American distribution map for this species.

Diagnostic Characters. – Average length, males, 10.0 mm (from anterior margin of head to tip of folded wings); females, 13.0 mm. Adults with yellowish color and darker markings on head; long cerci, about twice abdominal length. Male genitalia with paraprocts sharp, slender and recurved over tergum 10; tergum 10 with two brown patches of setae and a bilobed brown patch on tergum 9 (Fig. 120). Female subgenital plate produced about halfway across sternum 9; strongly sclerotized; posterior margin of subgenital plate rounded in most specimens (Fig. 129), but slightly or greatly emarginate (Fig. 130, 131) or even slightly pointed in some specimens (Fig. 132).

Nymphs with light color and faint longitudinal stripes on abdominal terga; light area within ocellar triangle not completely enclosed by darker area.

Needham and Claassen (1925), Frison (1942a), Gaufin *et al.* (1966) and Gaufin *et al.* (1972) figured the adult genitalia; Frison (1942a) figured the nymph.

Bionomics. – This species is apparently restricted to fairly large rivers. It is abundant in the Saskatchewan River System with adult emergence beginning in mid-June and lasting until about the end of July. The life-cycle appears to be univoltine since nymphs were absent from benthic collections for a time following the summer adult emergence.

Isoperla marylnia Needham and Claassen
(Fig. 137, 191)

Isoperla marylnia Needham and Claassen 1925: 148. – Claassen 1940: 203. – Frison 1942a: 330. – Harden and Mickel 1952: 203. – Hitchcock 1974: 202.

Isoperla marylnia is a common species of eastern Canada and United States. It has been reported from Virginia to New Brunswick, and west to Manitoba and Minnesota. This first Saskatchewan collection record (Fig. 191) is from Torch River, Jct. Hwy. 106, and Red Deer River near Chelan, Sask., Jct. Hwy. 23.

Diagnostic Characters. – Average length, males, 12.0 mm (from anterior margin of head to tip of folded wings); females, 13.0 mm. Adults with light color and brown markings; head with crescent-shaped light spot and two lateral light spots anterior to median ocellus. Male genitalia with paraprocts fairly long and slender, pointed at tips and recurved over tergum 10. Female subgenital plate produced less than halfway over sternum 9; with shallow median emargination (Fig. 137).

Nymphs with three possible distinct color phases. Light phase: mainly yellow with black lateral stripes on both posterior and anterior margins of each abdominal tergum. Intermediate phase: light markings laterally on each abdominal tergum with few light markings on head and pronotum. Dark phase: dark without yellow markings.

Needham and Claassen (1925) and Frison (1942a) figured the adult genitalia; Frison (1942a) figured the nymph. The three possible color phases of nymphs are apparently equally common, and may occur in the same population (Frison, 1942a). Only the light phase has been found in Saskatchewan specimens.

Bionomics. – A female nymph collected from Torch River, Jct. Hwy. 106 on April 12, 1976 emerged under laboratory conditions on June 15, 1976.

Isoperla patricia Frison
(Fig. 122, 136, 190)

Isoperla patricia Frison 1942a: 313. – Ricker 1943: 126. – Jewett 1959: 74. – Ricker 1964: 55. – Gaufin, Nebeker and Sessions 1966: 70. – Gaufin, Ricker, Miner, Milam and Hays 1972: 118.

Isoperla patricia, a common species in western Canada and United States, has been collected from British Columbia to California and Utah and east to Idaho, Montana and South Dakota. This first Saskatchewan record (Fig. 190) is from the South Saskatchewan River at Lemsford Ferry and the following Cypress Hills localities: Bear Creek, 10 mi S. of Piapot, Sask.; Shuard Creek, 11 mi S. of Piapot, Sask.; and Conglomerate Creek at Ravenscrag, Sask.

Diagnostic Characters. – Average length, males, 10.0 mm (from anterior margin of head to tip of folded wings); females, 12.5 mm. Most adult specimens with red pigmentation on abdominal segments.

Male genitalia with subanal lobes recurved upwards over tergum 10 and with slender, sharply pointed tips; posterior margin of sternum 9 with patches of short stout hairs (Fig. 122). Female subgenital plate produced about halfway over sternum 9 and deeply excavated in most specimens (Fig. 136).

Nymph with dark narrow band in center of abdominal terga bordered on each side by broader light band.

Frison (1942a), Gaufin *et al.* (1966) and Gaufin *et al.* (1972) figured the male and female genitalia; Frison (1942a) figured the nymph.

Bionomics. – This species appears to have a two-year life cycle in Saskatchewan. From a sample of 45 nymphs collected on June 3, 1975 at Shuard Creek, 11 mi S. of Piapot, Sask., 21 nymphs ranging in length from 4.0 mm to 9.5 mm (with an average length of 5.9 mm) had very little wing pad development and could not have emerged until the following year. Twenty-four mature nymphs ranging in length from 8.5 mm to 12.0 mm (with an average length of 10.3 mm) had full-grown wing pads and would have emerged the same year. There were several stages of nymphal development present at one time among the nearly mature specimens indicating little synchrony of emergence.

Isoperla petersoni Needham and Christensen
(Fig. 123, 124, 143, 192)

Isoperla petersoni Needham and Christensen 1927: 19. – Jewett 1959: 74. – Ricker 1964: 55. – Gaufin, Ricker, Miner, Milam and Hays 1972: 118.

Isoperla fontium, Neave 1929: 161. – Ricker 1943: 122.

Isoperla petersoni is found in western Canada and United States including Alberta, British Columbia, Utah and Montana. This first Saskatchewan record (Fig. 192) is from Mackenzie Creek near Bow River, Jct. Hwy. 165 and the stream at mile 83, Jct. Hwy. 106.

Diagnostic Characters. – Average length, males 12.5 mm (from anterior margin of head to tip of folded wings); females, 14.5 mm. Adults with yellow color and dark brown markings on head and thorax. Male genitalia with paraprocts slender, recurved over tenth tergum and darkly sclerotized (Fig. 123); aedeagus with slender sharp process forked at its base (Fig. 124), aedeagal process visible through sternum 9 of most specimens as dark rod-shaped structure; when not visible, aedeagal process may be exposed by dissecting away sternum 9. Female subgenital plate produced nearly halfway over sternum 9, and slightly emarginate at tip (Fig. 134).

Nymphs with longitudinal striped pattern on abdomen, but differ from other Saskatchewan *Isoperla* species by having broad central light band bordered on each side by dark band.

Neave (1929), Gaufin *et al.* (1966) and Gaufin *et al.* (1972) figured the female genitalia; Claassen (1931) figured the nymph.

Brachyptery has been reported in males of this species in Montana (Gaufin *et al.*, 1972) and in Utah (Gaufin *et al.*, 1966), but Saskatchewan specimens all have wings of normal length. The *Isoperla* species key for Montana nymphs given by Gaufin *et al.* (1972) states that nymphs of *Isoperla petersoni* lack a fringe of long hairs on the legs. Saskatchewan nymphs of this species all have a definite fringe of hairs on the legs though the hairs are shorter than in other species of this genus.

Bionomics. – Hales and Gaufin (1971) stated that this species is restricted to spring-fed streams or streams largely influenced by springs. Adult emergence was found to be relatively short, lasting about two weeks. In Saskatchewan, adults emerged in the end of June and early July of 1974.

Mackenzie Creek empties into the Bow River near Hwy. 165, and it is interesting that this species was found only in Mackenzie Creek. Samples from Bow River, even at the point of entry of Mackenzie Creek, showed numbers of *Isoperla transmarina*, but not *Isoperla petersoni*. In both rivers where

Isoperla petersoni was collected, larvae of Rhyacophilidae (Trichoptera) were also abundant though they are fairly uncommon in other Saskatchewan rivers.

Isoperla transmarina (Newman)

(Fig. 119, 135, 192)

Chloroperla transmarina Newman 1838: 499.

Isoperla fumosa, Neave 1933: 235.

Isoperla transmarina, Frison 1942a: 316. – Harden and Mickel 1952: 46. – Hitchcock 1974: 210.

Isoperla transmarina is a common North American species ranging from the Maritimes south to New Jersey and west to Minnesota, Manitoba and British Columbia. This first Saskatchewan report is from collections made at the following localities (Fig. 192): Little Red River, near Prince Albert, Sask.; stream 80 mi. N. of La Ronge, Sask. on Hwy. 102; Martineau River near Cold Lake; Cole Creek, Jct. Hwy. 104; Weyakwin River, Jct. Hwy. 2; Waskwei River, Jct. Hwy. 109; Mackay Creek, Jct. Hwy. 2; Nemeiben River, Jct. Hwy. 2; Bear River, Jct. Hwy. 106; Puskwakau River, Jct. Hwy. 106; Ballantyne River, Jct. Hwy. 106; Crean River, Jct. Hwy. 2; Churchill River at Wintego Lake Rapids, Otter Rapids, Iskwatam Lake, and Pita Lake; Montreal River, Jct. Hwy. 165 and at La Ronge, Sask.; Waskesiu River, Jct. Hwy. 2; Torch River, Jct. Hwy. 106; Overflowing River, Jct. Hwy. 109; Waterhen River, Jct. Hwy. 226; Broad Creek, Jct. Hwy. 104; McDougal Creek, Jct. Hwy. 120; North Saskatchewan River at Hwy. 5 (Borden Bridge); Bow River, Jct. Hwy. 165; Waddy River, Jct. Hwy. 102; Meeyomoot River, Jct. Hwy. 165; Arsenault River, Jct. Hwy. 104; Mistohay Creek, Jct. Hwy. 226; Nipekamew River, Jct. Hwy. 165; Caribou Creek, Jct. Hwy. 106; stream entering south end of Wollaston Lake, Jct. Hwy. 105; Fond du Lac River at Black Lake; Cluff Creek near Cluff Lake; Cub Creek, Jct. Hwy. 106; and Green Lake, Sask.

Diagnostic Characters. – Average length, males, 10.0 mm (from anterior margin of head to tip of folded wings); females, 14.0 mm. Adult with light brown and yellow coloration; light spot of ocellar triangle completely enclosed by darker areas in some specimens or may be slightly open posteriorly. Male genitalia with paraprocts sharply pointed, darkly sclerotized and recurved over tergum 10. Male abdominal terga with striped pattern, most easily seen on posterior segments (Fig. 119). Female subgenital plate truncate and produced about halfway over sternum 9.

Nymph with large light spot within ocellar triangle; longitudinal striped pattern on abdominal terga with central dark band bordered on each side by light stripes of about same width.

Ricker (1938) figured the male genitalia, and Neave (1933) figured the female genitalia (under the name *fumosa*). Frison (1942a) figured the nymph.

Bionomics. – Gaufin (1958) studied the effects of pollution on the Mad River in Ohio and found that the occurrence of *Isoperla transmarina* was limited entirely to the cleanest sections of the stream. Harden (1942) stated that nymphs seemed to prefer a habitat of matted leaves and vegetation trapped by submerged objects.

Harper (1973a) provided life cycle data for this species from southern Ontario. Adult emergence was fairly synchronous, beginning in early May and lasting 40 days. Emergence occurred in early morning and males emerged earlier than females. Oviposition was first observed in late May and early June. Egg hatching lasted from 34 to 43 days under simulated stream conditions. Early-instar nymphs were collected in the field in July which closely matched the laboratory incubation period. Rapid growth ensued until January when growth was minimal up to April. Growth was then continued and completed a few weeks before the May emergence.

DISCUSSION

Types of life histories and seasonal succession of Saskatchewan Plecoptera

The invertebrate benthos of flowing waters in temperate climates shows a clear succession of events as species appear and disappear from collections and one species after another completes its life cycle (Hynes, 1970). A life cycle classification will be employed to categorize how and when Saskatchewan stonefly species initiate and complete their development.

The system of classification proposed by Hynes (1961) can be applied to Saskatchewan stonefly life cycles. Basically a distinction is made between univoltine and seasonal species and non-univoltine or non-seasonal species. Non-seasonal species have individuals of all sizes present at all times while seasonal cycles show a distinct change of size distribution with time. Univoltine species are then separable into two groups. The "F" or fast type of cycle implies an embryonic diapause; species of "S" or slow type do not diapause. Each of these types can be further arbitrarily separated into four groups depending on the time of year when adults emerge. For example, group F₁ contains species of the fast seasonal type which emerge from mid-winter until April, adults of F₂ species emerge in May and June, F₃ species emerge in July and early August and F₄ species emerge in late August and in fall.

As can be seen from Table II, Saskatchewan Plecoptera have varied life histories and can contain, as far as is presently known, species representing all types except S₄ and F₃. A large number of species remain unclassified due to a paucity of life cycle data. Further life history studies on the uncategorized species will certainly increase the variety of types depicted.

The simplest seasonal type is S₁ in which embryonic development is immediate. Harper and Hynes (1972) further divided this category, separating species which undergo nymphal diapause from those which do not. For the sake of simplicity this grouping has not been followed here. Saskatchewan stoneflies with this type of life cycle are the so-called winter stoneflies.

Several Perlodidae and Chloroperlidae fall into the S₂ type. There are, however, still differences in the timing and deviation of adult emergence. For example, *Isoperla bilineata* emerges in late May; *Isoperla transmarina* emerges in early to mid-June, and *Hastaperla brevis* emerges throughout all of June.

Isoperla longiseta emerges in July and although it is not established for certain that an embryonic diapause is absent, the species probably is of the S₃ type.

Species with fast seasonal cycles undergo a long diapause at the onset of embryogenesis allowing them to survive the warm summer season as an underdeveloped egg. Saskatchewan stoneflies with this type of development include *Shipsa rotunda* emerging in late April (F₁), *Diura bicaudata* emerging in late spring (F₂) and *Amphinemura linda* and probably *Malenka californica* which emerge in late summer and autumn (F₄). *Amphinemura linda* may emerge as soon as early July in a few warm streams, but most often it does not emerge until mid-August, and thus will be considered type F₄.

Species which are listed in the uncertain section of Table I have inadequate life history information available for placement in any of the other categories.

Figure 193 presents the seasonal distribution of adult Plecoptera in Saskatchewan. The late winter and early spring fauna is evidently very rich, and this is succeeded by an equally diverse late spring and early summer fauna. There are few summer species and only *Amphinemura linda* and *Malenka californica* can be considered late summer and fall species. Several species, which have not been indicated in Fig. 193, are adventitious and their seasonal distributions are poorly known.

Table II. Types of life histories known in Saskatchewan Plecoptera. Data are from the literature and present study. The question marks (?) indicate that the life-cycle of the species is incompletely investigated and that it is placed in the most likely category from data available.

I. Non-seasonal species (life history longer than one year):

- Pteronarcys dorsata* (present study)
- Claassenia sabulosa* (present study)
- Acroneuria lycorias* (present study)
- Acroneuria abnormis* (present study)
- Hesperoperla pacifica* (present study)
- Paragnetina media* (Harper, 1973a; Heiman and Knight, 1970; Tarter and Krumholz, 1971; present study)

II. Seasonal species (life history of one year duration):

A. Slow type (no embryonic diapause):

S₁ (adult emergence from mid-winter until April)

- Zapada cinctipes* (Clifford, 1969)
- Paracapnia angulata* (Harper and Hynes, 1970; Harper and Hynes, 1972)
- ? *Oemopteryx fosketti*
- ? *Capnia confusa*
- ? *Capnia coloradensis*
- ? *Capnia gracilaria*
- ? *Utacapnia trava*

S₂ (adult emergence in May and June):

- Isoperla transmarina* (Harper, 1973a)
- ? *Isoperla bilineata*
- ? *Isoperla petersoni*
- ? *Isoperla patricia*
- ? *Skwala parallela*
- ? *Hastaperla brevis*
- ? *Triznaka signata*
- ? *Isogenoides frontalis*
- ? *Isogenoides colubrinus*

S₃ (adult emergence in July and early August):

- ? *Isoperla longiseta*

B. Fast type (Embryonic diapause):

F₁ (adult emergence from mid-winter until April):

- Shipsa rotunda* (Harper, 1973b)

F₂ (adult emergence in May and June):

- Diura bicaudata* (Brinck, 1949)

F₄ (adult emergence in late August and fall):

- Amphinemura linda* (Harper, 1973b)
- ? *Malenka californica*

III. Species of uncertain life cycle.

*Perlesta placida**Suwallia lineosa**Pteronarcella badia**Isoperla decolorata**Isoperla marlynia**Nemoura rickerti**Podmosta delicatula**Paraleuctra vershina**Leuctra ferruginea**Capnia vernalis**Isocapnia crinita**Isocapnia missouri**Arcynopteryx compacta*

Although the period of adult occurrence overlaps for several species, the timing of their maximum abundance differs.

The differences in stonefly life histories and adult seasonal successions are important in limiting interspecific and intraspecific competition and allowing the coexistence of several stonefly species in the same stream.

Winter stoneflies, which concentrate the largest proportion of their nymphal growth in fall and winter, have utilized several ecological opportunities as Harper and Hynes (1972) point out. Food, in the form of dead plant matter, is especially abundant in this time of year. Also, few other stream insects are active during this season. Species which grow rapidly in early spring and undergo nymphal diapause in summer are able to use an abundant spring food supply in form of dead leaves which have soaked right through the winter.

Many carnivorous Perlodidae and Chloroperlidae show a wide range of size-frequency distributions in a given sample indicating the simultaneous co-existence of specimens of different sizes. Harper (1973a) argues that this has the result of lessening intraspecific competition because it provides predatory individuals with a wider variety of prey organisms.

Some related species of the same genus or family show a distinct succession of adults, with the obvious advantage of limiting possible mating encounters.

Saskatchewan stonefly species show a variety of life history patterns and adult seasonal distributions. Life cycle differences enable the co-existence of several stonefly species in the same stream, and a succession of adults permits maintenance of a higher level of diversity.

Origin and past dispersal of Saskatchewan Plecoptera

In order to reconstruct the faunal history of a region it is necessary to integrate information of the geographical and ecological distribution of existent species with knowledge of the geological and climatic history of the area. To determine past dispersals of species it is requisite to assume that each species is now found in the same type of habitat which it occupied in the past and that geographical changes in the distribution of a species' habitat have also affected the possible range of that species. Also, it is assumed that non-glaciated areas presently occupied by a species represent refugia or regions where the species was able to pass the glacial maximum (Larson, 1975).

The destructive results of the Pleistocene glaciation had a major effect in shaping the distributional history of the extant fauna. There were four major glaciations in the Pleistocene but the last of the glacial advances, the Wisconsin, obliterated the effects of the previous glaciations and virtually eliminated the fauna of Saskatchewan. The present-day faunal composition of areas previously ice-covered originated with the retreat of Wisconsin ice.

In order to arrive at a reasonable explanation of post-glacial stonefly dispersal into Saskatchewan, several events of the Wisconsin glaciation will be discussed including the full extent of the ice sheets and locations of possible refugia, subsequent retreat of ice from the glacial maximum and the important post-glacial lakes and river systems and their development to the present.

The Wisconsin glaciation began about 50,000 years before present (B.P.) and extended about 11,000 years B.P. (McPhail and Lindsey, 1970). At its maximum extent (17,000 years B.P.) almost all of Saskatchewan was ice-covered by the Laurentide ice sheet except Cypress Hills and a small area in southcentral Saskatchewan on the present-day Canada-United States border (Prest, 1968). By about 14,000 years B.P., Prest (1968) suggests that the glaciers had retreated from southwestern Saskatchewan and by 13,000 years B.P. most of southcentral Saskatchewan was also ice-free. Two-thirds of Saskatchewan was ice-free about 10,000 years B.P.

As the Laurentide ice sheet began its retreat, Glacial Lake Agassiz formed over roughly 200,000 square miles of the provinces of Ontario, Manitoba and Saskatchewan and the states of Minnesota, North Dakota and South Dakota (Elson, 1967). The morphometry and the outlets of Lake Agassiz changed as the glaciers advanced and retreated for short periods. Elson (1967) noted that the lake originally drained south to the Mississippi River System and later to the Great Lakes, and to the Athabasca River in the northeast. As the ice receded, the lake drained north to Hudson Bay.

The Saskatchewan River System began to flow south, prior to 12,000 years B.P., into the Big Muddy-Missouri System because the ice front prevented a northerly flow (Elson, 1967). Further retreat of the ice sheet diverted its course to the Souris-Lake Agassiz drainage, and then to the Qu'Appelle Valley-Assiniboine River drainage. Finally, the ice retreated sufficiently to allow a northern drainage to Hudson Bay.

The present-day stonefly fauna of Saskatchewan is the result of post-glacial dispersal from ice-free refugia. The Cypress Hills was unglaciated (Westgate, 1964), and could have served as a refugium. Also, there were unglaciated areas in Alaska and Yukon which served as important refugia for some organisms (McPhail and Lindsey, 1970; Munroe, 1956). Three important refugia formed south of the continental ice sheet: the Pacific refugium west of the continental divide, the Mississippi comprised of the Missouri River and Upper Mississippi River Systems and the Atlantic refugium (McPhail and Lindsey, 1970).

Ricker (1964) proposed that the most likely species which survived glaciation in the northwestern refuge of Alaska and Yukon are the present-day tundra species: *Nemoura arctica*, *Capnia nearctica*, *Isoperla decolorata*, *Diura bicaudata* and *Arcynopteryx compacta*. These species have since migrated as far east as Hudson Bay but as yet have been unable to pass around its southern extremity. The latter three species have been found in Saskatchewan: *Diura bicaudata* and *Arcynopteryx compacta* in the northern boreal region and a single specimen of *Isoperla decolorata* collected in the North Saskatchewan River.

The collection of *Diura bicaudata* in northern Saskatchewan and a record from approximately the same latitude near Hudson Bay in Manitoba represent the most southerly known point to which this species has been able to penetrate the boreal forest. *Arcynopteryx compacta*, however,

has not only been collected in northern Canada west of Hudson Bay, but also from the Great Lakes, New Hampshire, southern Alberta and Wyoming. Ricker (1964) suggests that the species must have lived in Glacial Lake Agassiz and dispersed eastward when the lake drained to the Great Lakes. The common factor in the distribution of *Arcynopteryx compacta* is that it occurs principally in cold lakes. *Isoperla decolorata* has crossed the tundra and boreal forest, reaching its most southerly distribution on the Saskatchewan parkland. *Nemoura rickeri* has been collected previously only in Alaska and also probably dispersed from a northwestern refugium.

A number of species reach their most westerly ranges in the boreal regions of Saskatchewan, Alberta and northeastern British Columbia, and are abundant in nonglaciated areas of eastern North America. These species probably originated in an eastern boreal refugium and dispersed to the north and west. Saskatchewan species with this type of distribution include *Acroneuria lycorias*, *Perlesta placida*, *Paragnetina media*, *Pteronarcys dorsata*, *Isoperla transmarina*, *Isoperla marlynia*, *Shipsa rotunda*, *Hastaperla brevis*, *Taeniopteryx nivalis*, *Amphinemura linda*, *Isogenoides frontalis*, and *Leuctra ferruginea*. The extent to which southeastern species have invaded Saskatchewan varies from species to species. *Paragnetina media*, *Taeniopteryx nivalis* and *Isoperla marlynia* are found in northeastern Saskatchewan but not in the northwest. *Perlesta placida* occurs only in eastcentral Saskatchewan. Other species range entirely across the northern part of the province and beyond: *Hastaperla brevis* extends to the Mackenzie River, *Amphinemura linda* enters southern Yukon; *Isoperla transmarina* reaches northern British Columbia and *Shipsa rotunda* extends to the Mackenzie River delta. *Pteronarcys dorsata*, an exceptionally widespread species, occurs across Canada except in southern British Columbia and on the tundra.

Several species are widespread in the mountains of western North America and also occur in Saskatchewan boreal regions. They probably survived glaciation in the western portion of the southern North American refugium and dispersed north and east from the eastern border of the Rockies. Species with this type of distribution are: *Pteronarcella badia*, *Isoperla petersoni*, *Capnia confusa*, *Capnia coloradensis*, *Capnia vernalis*, *Utacapnia trava*, *Claassenia sabulosa*, *Zapada cinctipes*, *Malenka californica* and *Triznaka signata*. On reaching the boreal forest, these species moved eastward in varying degrees: *Pteronarcella badia* and *Triznaka signata* occur only in northwestern Saskatchewan and the rest of the species have reached northeastern Saskatchewan.

The Cypress Hills remained unglaciated in the Wisconsin (McPhail and Lindsey, 1970) and there is no reason to believe that they could not have harbored stoneflies even though the area was completely surrounded by ice. Westgate (1964) provided evidence in Cypress Hills of ponds with vegetation and animals, not only at the ice edge, but actually on the ice surface where debris had accumulated to provide a suitable substrate.

Bird (1962), studying bryophytes, Russell (1951), studying land snails and Yeatman (1967) studying pines, demonstrated that the Cypress Hills flora and fauna has its principal affinities with the Rocky Mountains. Russell (1951) contended that most or all of the land snails entered the Cypress Hills postglacially across a "bridge" of suitable climatic and edaphic conditions connected with the mountains. The bridge later disappeared as the glaciers retreated further and the climate warmed. This proposal agrees with the statements of Love (1959) regarding the direction of floral movement across the southern prairies.

Cypress Hills stoneflies are all montane species and their affinities are with present-day species of the Rocky Mountains. Though not a likely possibility, these stoneflies could have been present in the Cypress Hills prior to the Wisconsin and passed the glacial maximum in the Cypress Hills refugia. This proposal assumes that the area was connected to the mountains by a similar type of

climatic and edaphic "bridge" sometime prior to the Wisconsin glaciation. Though little is known of pre-Wisconsin geography, the formation of such a connection from the Cypress Hills to the mountains could as easily have occurred after pre-Wisconsin glaciations just as it could following the Wisconsin glaciation.

The second, more likely origin of Cypress Hills Plecoptera could be by post-Wisconsin dispersal to the area from the Rockies by a connecting bridge of montane climatic and edaphic conditions which is proposed to have formed as the ice retreated. As the climate warmed and the bridge disappeared, the stoneflies were separated from their parent population.

Montane species occurring in the Cypress Hills include *Hesperoperla pacifica*, *Podmosta delicatula*, *Suwallia lineosa*, *Paraleuctra vershina*, *Capnia gracilaria*, *Isocapnia crinita*, *Isocapnia missouri*, *Zapada cinctipes*, *Utacapnia trava*, *Skwala parallela* and *Isoperla patricia*.

Cypress Hills stoneflies have been unsuccessful in dispersing to, or populating, surrounding prairie rivers either because of the large expanses of prairie separating them from the rivers or because of their ecological preference for cool water. The single exception is *Isoperla patricia* which has been collected at Lemsford Ferry on the South Saskatchewan River, about 80 miles north of Cypress Hills.

A group of species occurs in the Saskatchewan boreal forest region and in the Cypress Hills. All are widespread in the western North American mountains including the western portion of the southern North American refugium. These separated Saskatchewan populations probably have a dual origin. The Cypress Hills fauna likely originated by a connection to the mountains either in pre-Wisconsin or post-Wisconsin time. The western species occurring in the boreal forest probably dispersed east and north from the eastern border of the Rockies. Species showing this distribution are *Zapada cinctipes*, *Utacapnia trava* and *Skwala parallela*. It is unlikely that these species originated from the Cypress Hills refugium and dispersed northward because they do not occur either in the prairie rivers or in rivers on the southern margin of the boreal forest in Saskatchewan.

Some of the prairie and parkland fauna consists of a northern Great Plains component. These species occur in the northern part of the Great Plains east of the Rockies and west of the Mississippi. Species showing this form of distribution are *Isoperla longiseta*, *Isoperla bilineata* and *Acroneuria abnormis*. These species probably entered the Saskatchewan River System when it flowed south to the Big Muddy-Missouri Systems. The southeastern and southcentral prairie species then had a direct aquatic dispersal route, and subsequent changes in drainage patterns have isolated Saskatchewan River populations from their parent populations.

Oemopteryx foscetti occurs in the Saskatchewan River System and also in the Colorado System. It probably dispersed northward in a manner similar to that proposed by Lehmkuhl (1976) for the mayfly *Anaetris eximia* Edmunds. A direct aquatic invasion route is not evident, but the species could possibly have crossed from the Colorado to the Missouri System in Wyoming and then entered the Saskatchewan System from tributaries of the Missouri in southern Alberta and Saskatchewan.

The present-day stonefly fauna of Saskatchewan is of diverse origins, showing a variety of distributional patterns and histories. Northern glacial refugia contributed to a small percentage of the post-glacial stonefly re-colonization of Saskatchewan. The majority of the present fauna was derived from refugia south of the main Wisconsin ice sheets.

SUMMARY AND CONCLUSIONS

Saskatchewan has a diverse stonefly fauna which comprises at least 41 species. Nymphs were reared in the laboratory in order to associate them with known adults and this has enabled the first nymphal descriptions of the following species: *Oemopteryx fosketti*, *Triznaka signata*, *Suwallia lineosa*, *Isoperla decolorata*, *Nemoura rickeri*, *Malenka californica*, *Podmosta delicatula*, *Capnia coloradensis*, *Capnia confusa* and *Capnia gracilaria*. Keys are provided for most nymphs and all adults except females of *Isogenoides frontalis* and *Isogenoides colubrinus*.

The life cycle classification devised by Hynes (1961) was used to categorize the life histories of several Saskatchewan Plecoptera. Both univoltine and non-univoltine life cycles are evident in Saskatchewan species with univoltine types ranging from slow with an early emergence (S_1) to fast with a late emergence (F_4). Winter stoneflies all seem to be in type S_1 in which an embryonic diapause is absent and adults emerge in late winter and early spring. The majority of non-winter species appear to belong to type S_2 in which embryonic diapause is also absent but adult emergence is later in May and June. Few species have been classified as fast seasonal types with an embryonic diapause. At present, life cycle types S_4 and F_3 are unknown in Saskatchewan species. Only 13 of the 41 stonefly species known in the province have been definitely classified, indicating the large amount of research required to determine all the life cycles of Saskatchewan Plecoptera.

All or most of the present-day Saskatchewan stonefly fauna originated with the retreat of the Wisconsin Laurentide Ice Sheet and the subsequent recolonization of the province by species from ice-free regions to the north and south. Five probable origins have been proposed for the extant fauna. The Cypress Hills fauna has its affinities with the Rocky Mountains and was derived by a connective bridge of flora and fauna which formed either after the Wisconsin or following earlier glaciations. The fauna to the extreme north of the province has tundra elements and is likely derived from a northwestern refugium. The boreal fauna is derived from southern North American refugia in the northeast and northwest and the prairie fauna is derived chiefly from the southcentral North American refugium.

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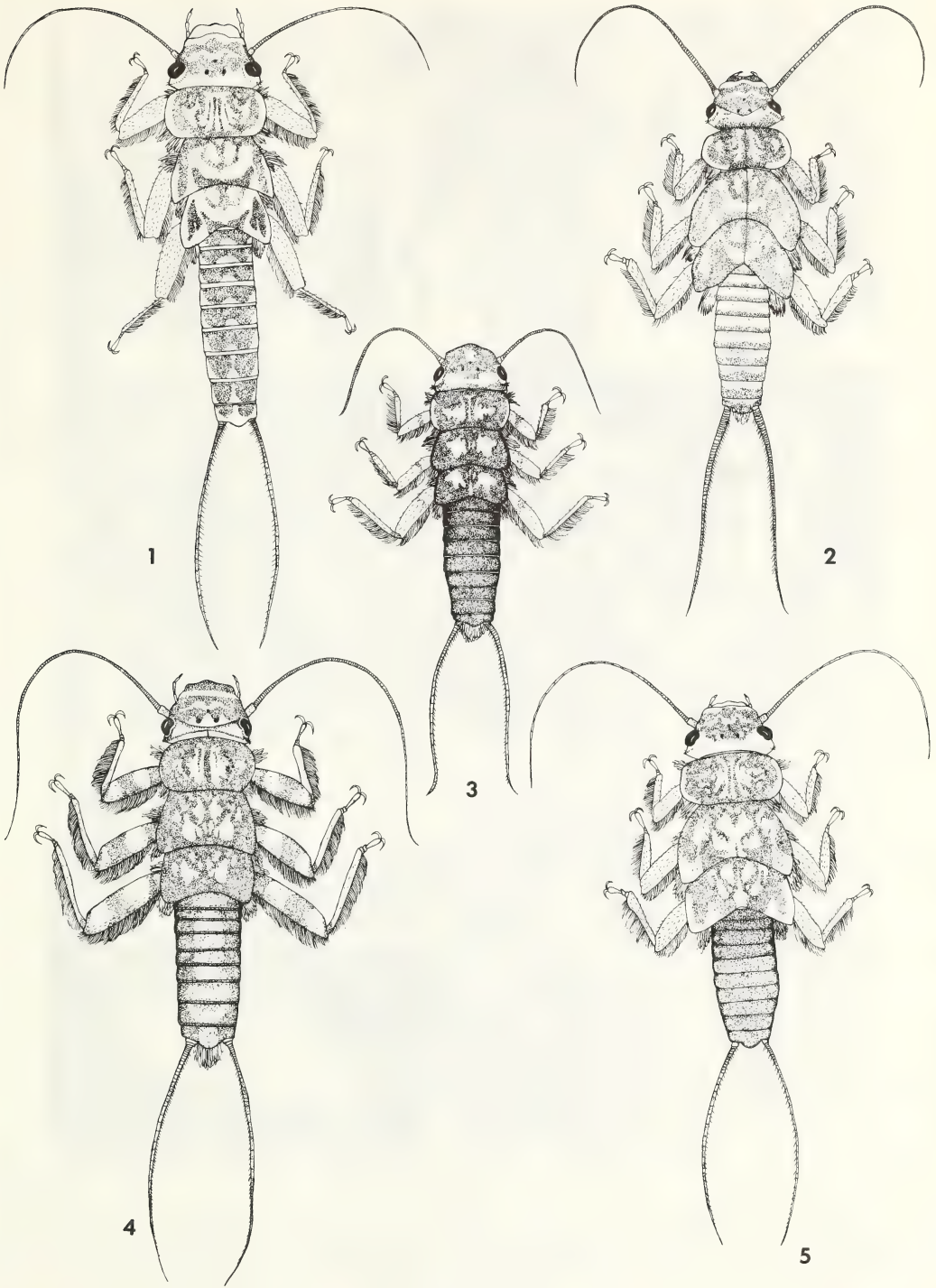
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Figures 1–5. Nymphs of Perlidae. Fig. 1, *Acroneuria abnormis*; Fig. 2, *A. lycorias*; Fig. 3, *Hesperoperla pacifica*; Fig. 4, *Claassenia sabulosa*; Fig. 5, *Paragnetina media*.

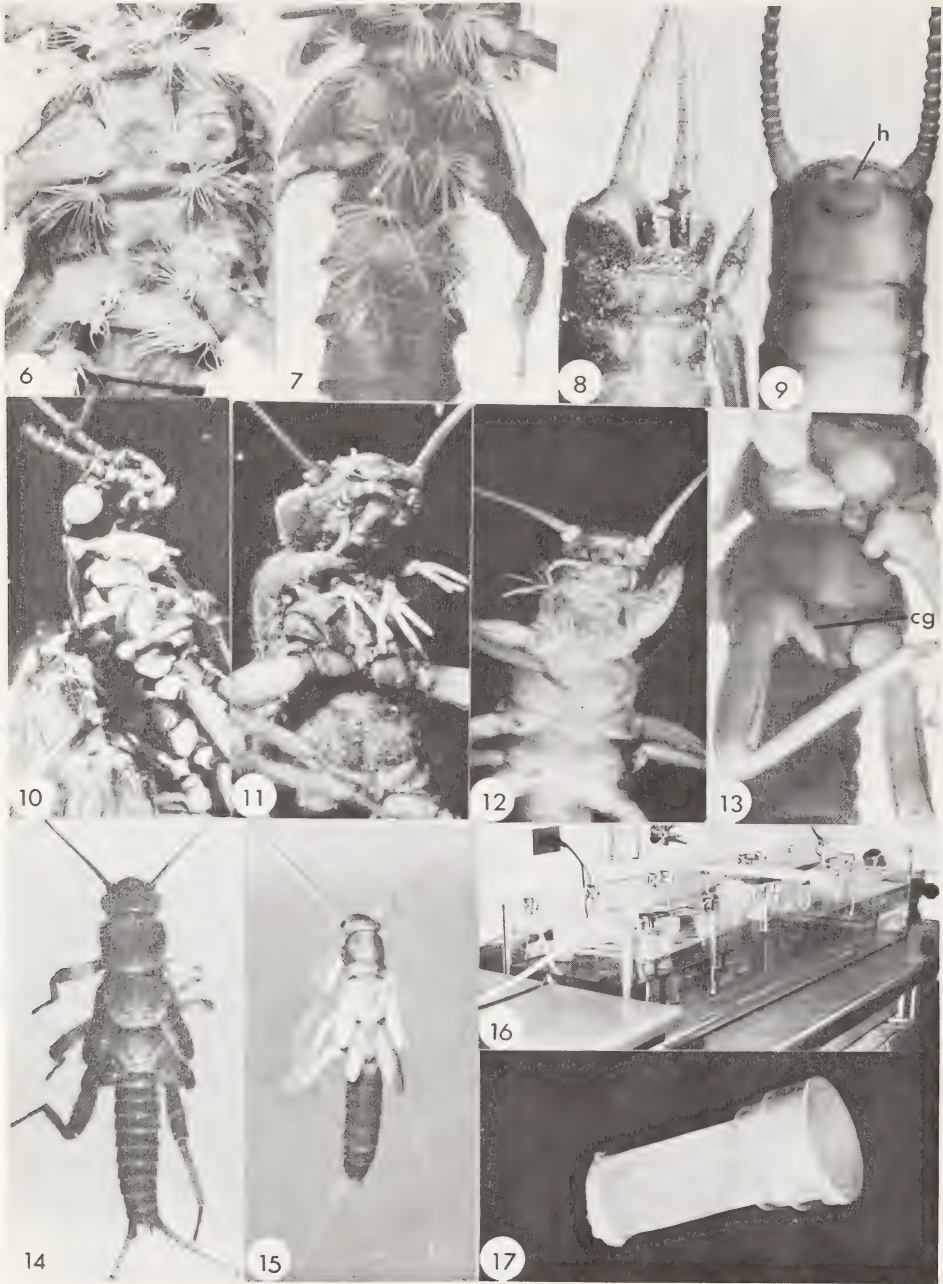
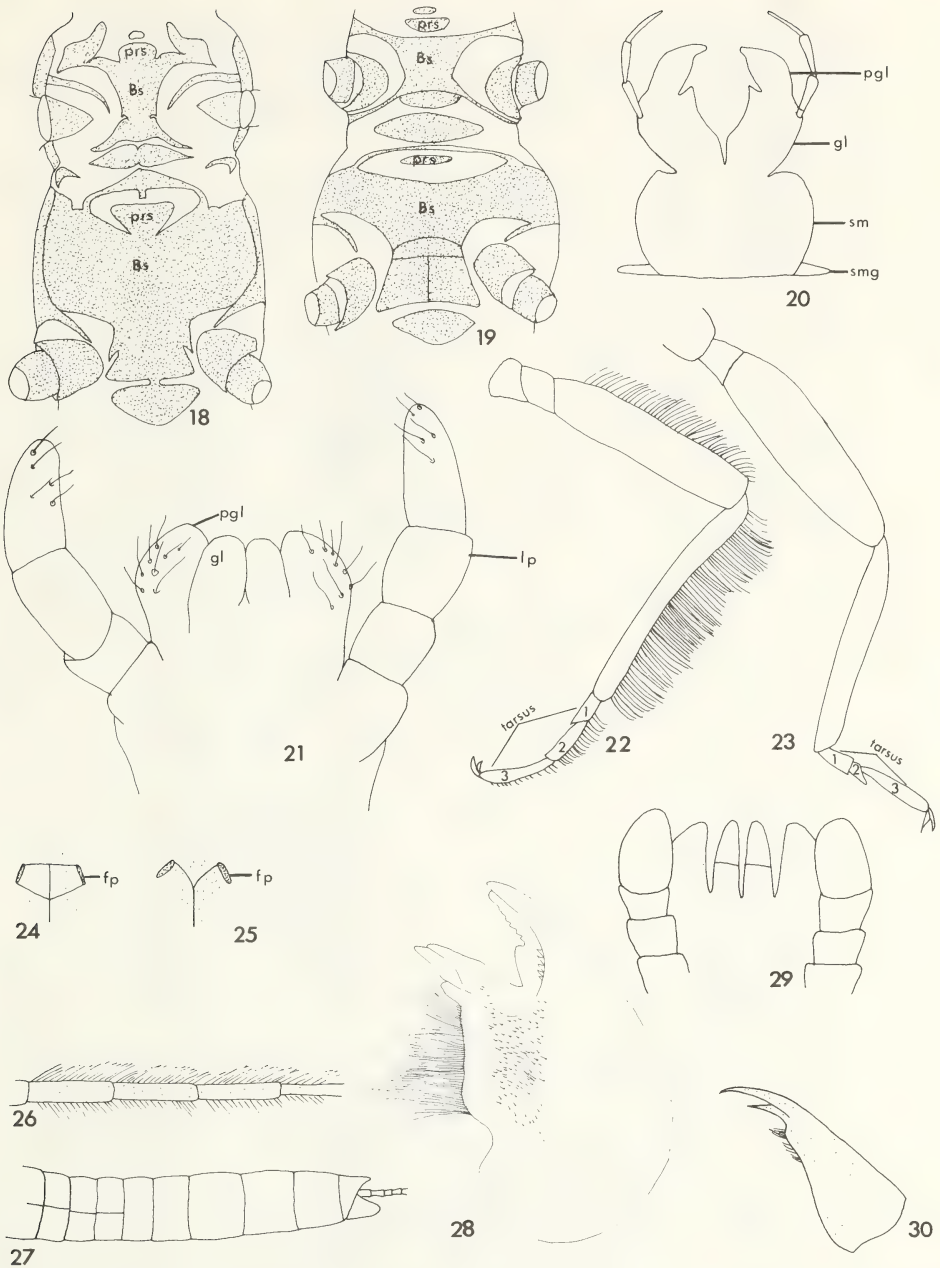
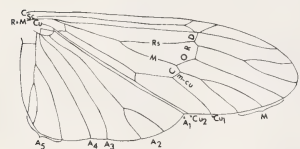
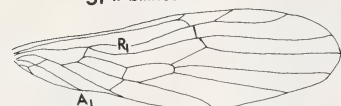
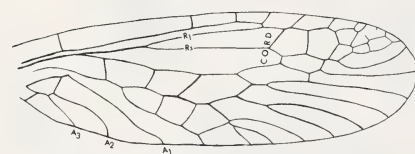


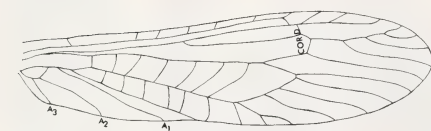
Fig. 6–17. Fig. 6, Nymph of *Pteronarcys dorsata* (ventral) showing gills on the first two abdominal segments; Fig. 7, Nymph of *Pteronarcella badia* (ventral) showing gills on the first three abdominal segments; Fig. 8, Terminal abdominal segments of *Claassenia sabulosa* (male, dorsal) showing hooks on the tenth tergite; Fig. 9, Terminal abdominal segments of *Acroneuria abnormis* (male, ventral) showing hammer (h); Fig. 10, Adult of *Zapada cinctipes* (lateral) showing cervical gill remnants; Fig. 11, Nymph of *Z. cinctipes* (ventral) showing cervical gills; Fig. 12, Nymph of *Amphinemura linda* (ventral) showing cervical gills; Fig. 13, Nymph of *Taeniopteryx nivalis* (ventral) showing coxal gill (cg); Fig. 14, Nymph of *Z. cinctipes* (dorsal); Fig. 15, Nymph of *Capnia gracilaria* (dorsal); Fig. 16, Rearing apparatus; Fig. 17, Rearing container.



Figures 18–30. Fig. 18, Prothoracic and mesothoracic sterna of *Isocapnia crinita*, showing the basisternum (Bs) and presternum (prs); Fig. 19, Prothoracic and mesothoracic sterna of *Paracapnia angulata*, showing basisternum (Bs) and presternum (prs); Fig. 20, Nymphal labium of *Isoegenoides colubrinus*, showing paraglossa (pgl), glossa (gl), submentum (sm) and submental gill (smg); Fig. 21, Nymphal labium of *Leuctra ferruginea*, showing paraglossa (pgl), glossa (gl) and labial palpus (lp); Fig. 22, Nymphal hindleg of *Oemopteryx fosketti*; Fig. 23, Nymphal hindleg of *Capnia gracilaria*; Fig. 24, Nymphal mesothoracic ridge pattern of *Isoegenoides colubrinus*, showing the furcal pit (fp); Fig. 25, Nymphal mesothoracic ridge pattern of *Skwala parallela*, showing the furcal pit (fp); Fig. 26, Distal cercal segments of *Isocapnia crinita* nymph; Fig. 27, Nymphal abdomen of *Leuctra ferruginea*; Fig. 28, Nymphal mandible of *Skwala parallela*; Fig. 29, Nymphal labium of *Zapada cinctipes*; Fig. 30, Nymphal maxilla of *Diura bicaudata*.

31 *I. bilineata*33 *P. angulata*

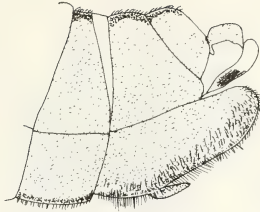
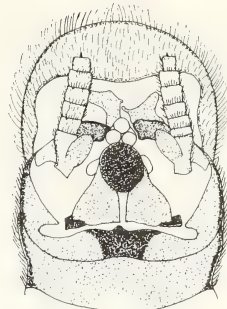
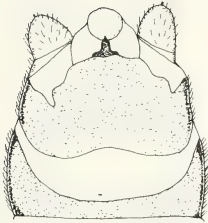
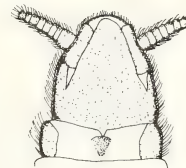
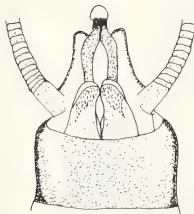
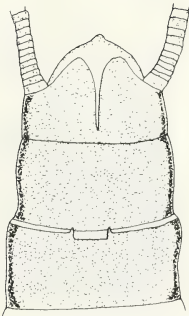
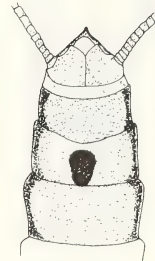
35 *S. parallela*

38 *I. colubrinus*32 *H. brevis*34 *P. vershina*36 *L. ferruginea*

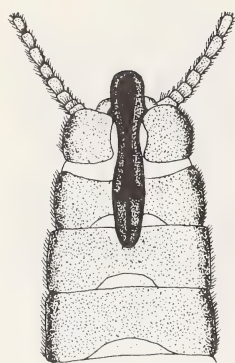
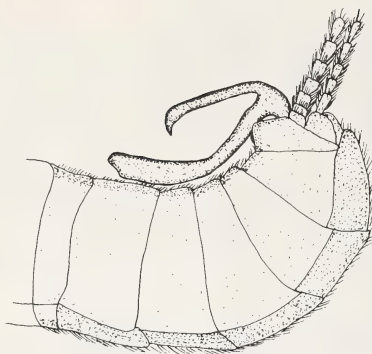
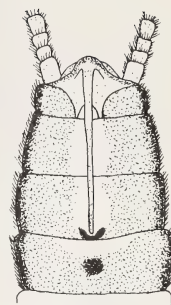
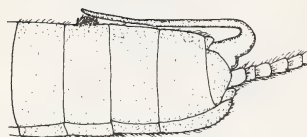
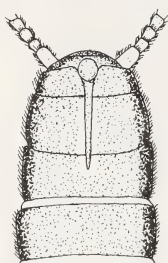
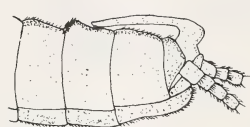
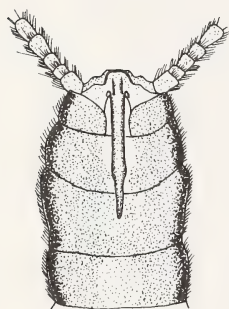
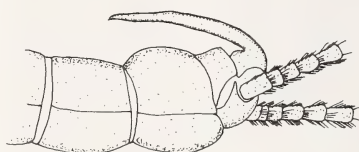
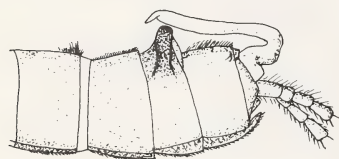
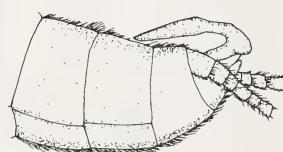
37 *C. confusa*

39 *I. crinita*

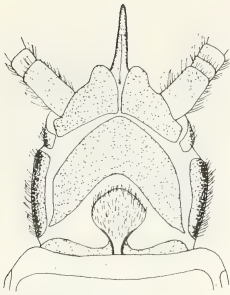
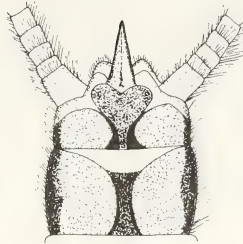
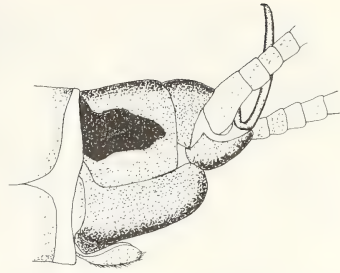
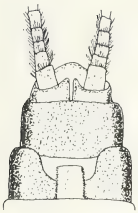
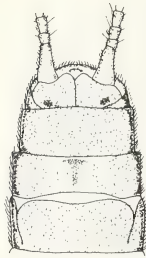
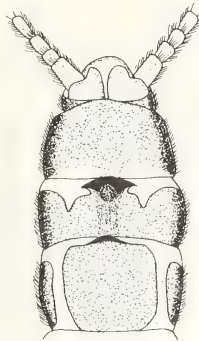
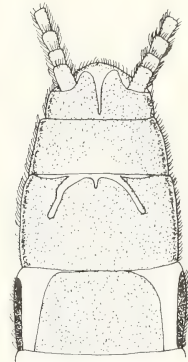
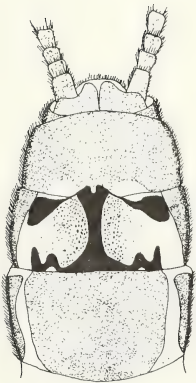
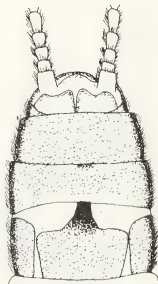
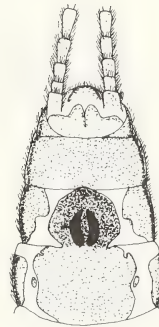
Figures 31 – 39. Wings of Plecoptera. Fig. 31, *Isoperla bilineata*; Fig. 32, *Hastaperla brevis*; Fig. 33, *Paracapnia angulata*; Fig. 34, *Paraleuctra vershina*; Fig. 35, *Skwala parallela*; Fig. 36, *Leuctra ferruginea*; Fig. 37, *Capnia confusa*; Fig. 38, *Isogenoides colubrinus*; Fig. 39, *Isocapnia crinita*.

40 *T. nivalis*41 *T. nivalis*42 *O. foscetti*43 *T. nivalis*44 *T. nivalis*45 *O. foscetti*46 *P. dorsata*47 *P. dorsata*48 *P. dorsata*49 *P. badia*

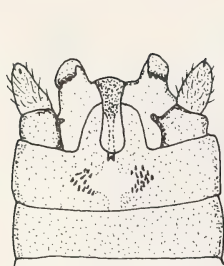
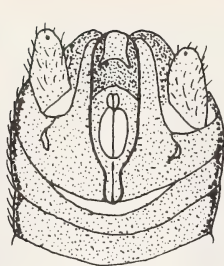
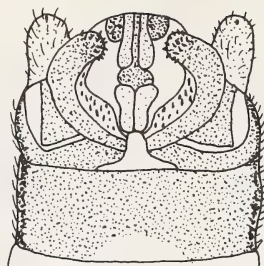
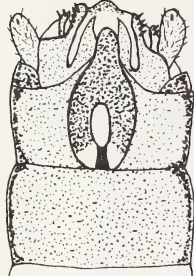
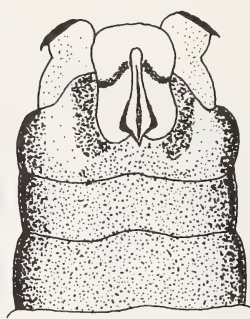
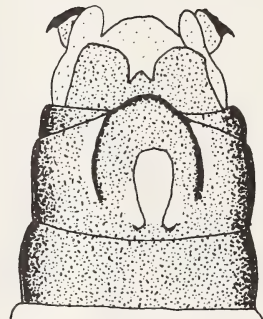
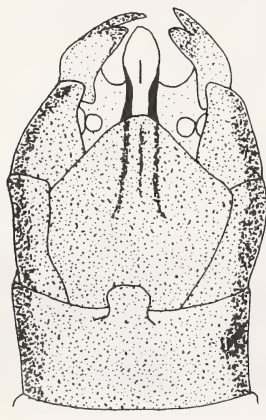
Figures 40 – 49. Genitalia of Taeniopterygidae and Pteronarcidae. Fig. 40, *Taeniopteryx nivalis* (male, lateral); Fig. 41, *T. nivalis* (male, ventral with 9th sternite removed to show aedeagus and subanal lobes); Fig. 42, *Oemopteryx foscetti* (male, dorsal); Fig. 43, *T. nivalis* (male, dorsal); Fig. 44, *T. nivalis* (female, ventral); Fig. 45, *O. foscetti* (female, ventral); Fig. 46, *Pteronarcys dorsata* (male, dorsal); Fig. 47, 48, *P. dorsata* (female, ventral showing variation in subgenital plates); Fig. 49, *Pteronarcella badia* (female, ventral).

50 *U. trava*51 *U. trava*52 *C. gracilaria*53 *C. gracilaria*54 *C. confusa*55 *C. confusa*56 *C. vernalis*57 *C. vernalis*58 *C. coloradensis*59 *C. coloradensis*60 *P. angulata*61 *P. angulata*

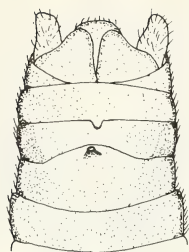
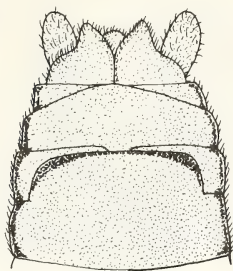
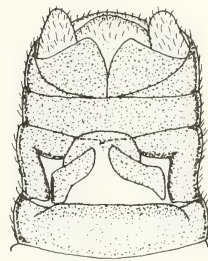
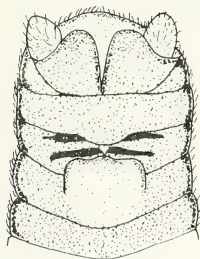
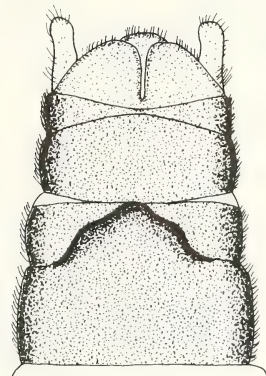
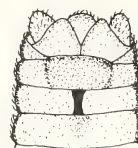
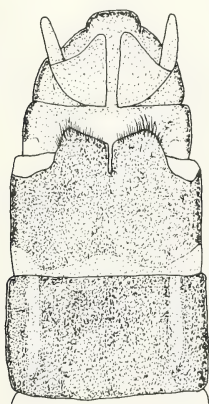
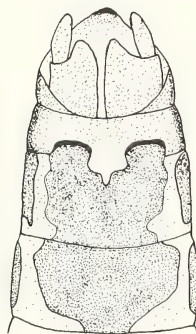
Figures 50 – 61. Male genitalia of Capniidae. Fig. 50, *Utacpnia trava* (dorsal); Fig. 51, *U. trava* (lateral); Fig. 52, *Capnia gracilaria* (dorsal); Fig. 53, *C. gracilaria* (lateral); Fig. 54, *C. confusa* (dorsal); Fig. 55, *C. confusa* (lateral); Fig. 56, *C. vernalis* (dorsal); Fig. 57, *C. vernalis* (lateral); Fig. 58, *C. coloradensis* (dorsal); Fig. 59, *C. coloradensis* (lateral); Fig. 60, *Paracpnia angulata* (dorsal); Fig. 61, *P. angulata* (lateral).

62 *I. crinita*63 *I. crinita*64 *I. crinita*65 *I. crinita*66 *I. missouri*67 *C. vernalis*68 *P. angulata*69 *U. trava*70 *C. confusa*71 *C. coloradensis*72 *C. gracilaria*

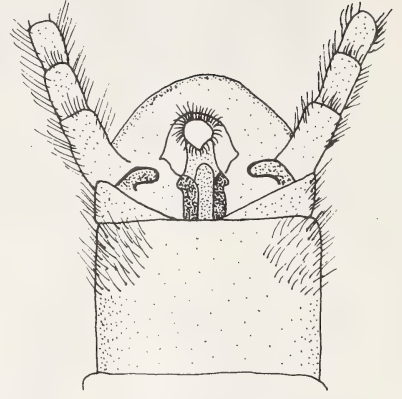
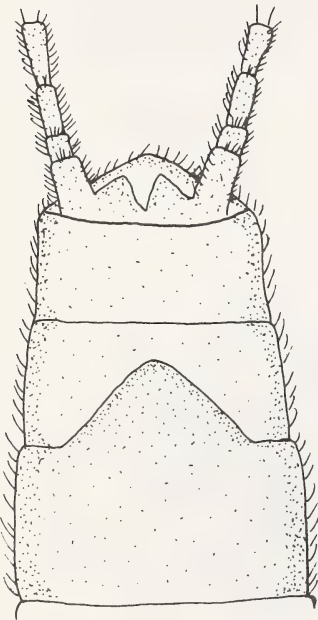
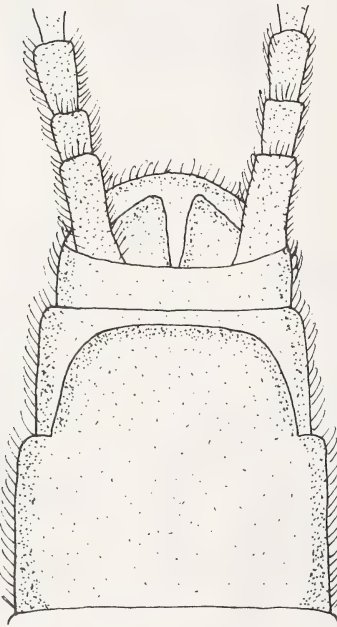
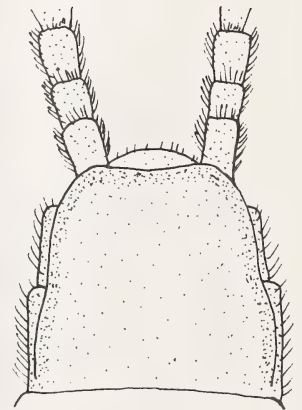
Figures 62 – 72. Genitalia of Capniidae. Fig. 62, *Isocapnia crinita* (male, ventral); Fig. 63, *I. crinita* (male, dorsal); Fig. 64, *I. crinita* (male, lateral); Fig. 65, *I. crinita* (female, ventral); Fig. 66, *I. missouri* (female, ventral); Fig. 67, *Capnia vernalis* (female, ventral); Fig. 68, *Paracapnia angulata* (female, ventral); Fig. 69, *Utacapnia trava* (female, ventral); Fig. 70, *Capnia confusa* (female, ventral); Fig. 71, *C. coloradensis* (female, ventral), Fig. 72, *C. gracilaria* (female, ventral).

73 *M. californica*74 *Z. cinctipes*75 *S. rotunda*76 *P. delicatula*77 *A. linda*78 *A. linda*79 *N. rickerei*80 *N. rickerei*81 *P. vershina*82 *P. vershina*83 *P. vershina*84 *L. ferruginea*

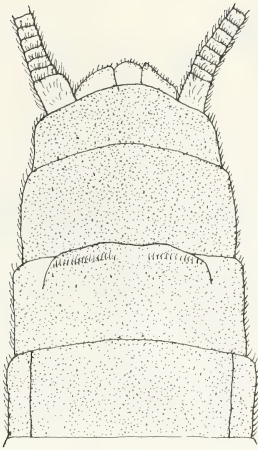
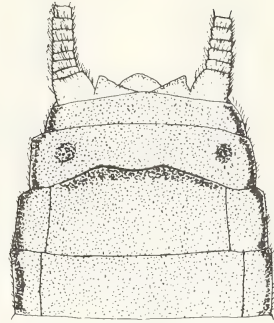
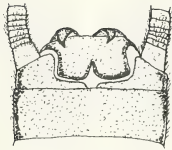
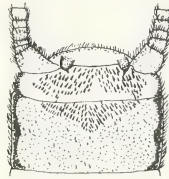
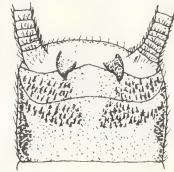
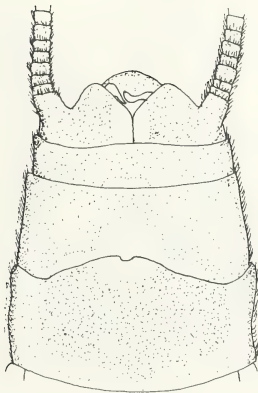
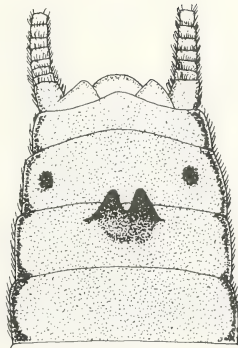
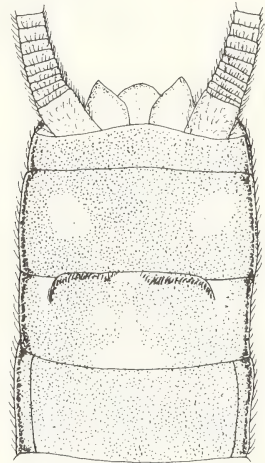
Figures 73 – 84. Male genitalia of Nemouridae and Leuctridae. Fig. 73, *Malenka californica* (dorsal); Fig. 74, *Zapada cinctipes* (dorsal); Fig. 75, *Shpsa rotunda* (dorsal); Fig. 76, *Podmosta delicatula* (dorsal); Fig. 77, *Amphinemura linda* (dorsal); Fig. 78, *A. linda* (ventral); Fig. 79, *Nemoura rickerei* (dorsal); Fig. 80, *N. rickerei* (ventral); Fig. 81, *Paraleuctra vershina* (dorsal); Fig. 82, *P. vershina* (ventral); Fig. 83, *P. vershina* cercus (lateral); Fig. 84, *Leuctra ferruginea* (dorsal).

85 *M. californica*86 *Z. cinctipes*87 *S. rotunda*88 *A. linda*89 *N. rickeri*90 *P. delicatula*91 *P. vershina*92 *L. ferruginea*

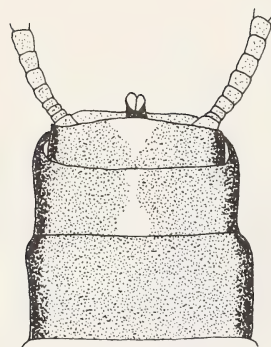
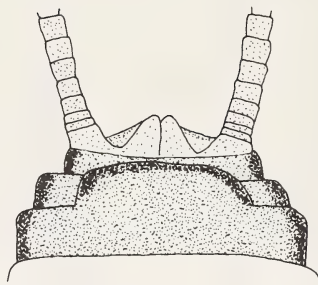
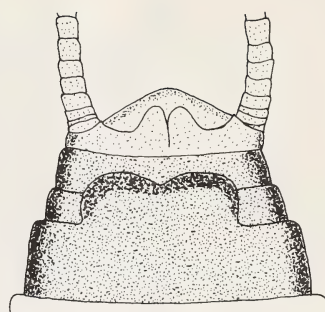
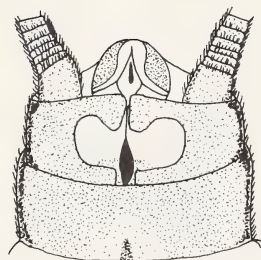
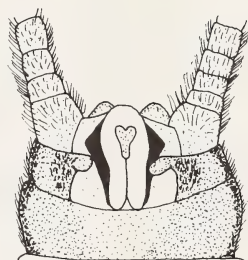
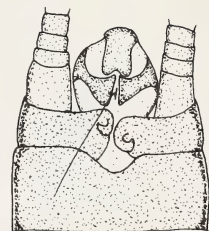
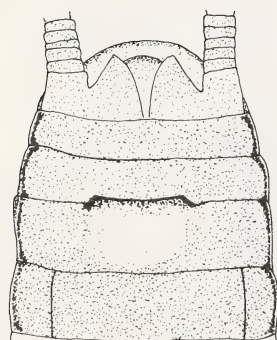
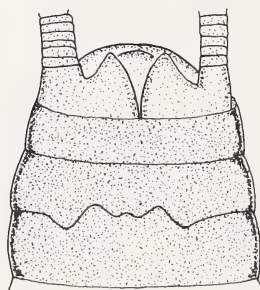
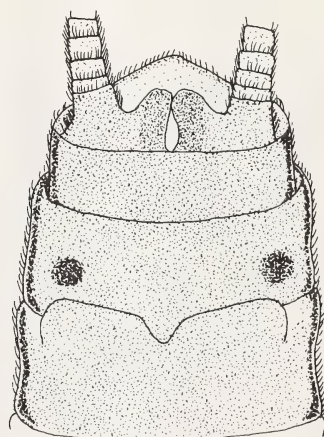
Figures 85 – 92. Female genitalia of Nemouridae and Leuctridae. Fig. 85, *Malenka californica* (ventral); Fig. 86, *Zapada cinctipes* (ventral); Fig. 87, *Shippa rotunda* (ventral); Fig. 88, *Amphinemura linda* (ventral); Fig. 89, *Nemoura rickeri* (ventral); Fig. 90, *Podmosta delicatula* (ventral); Fig. 91, *Paraleuctra vershina* (ventral); Fig. 92, *Leuctra ferruginea* (ventral).

93 *H. brevis*94 *T. signata*95 *S. lineosa*96 *H. brevis*97 *T. signata*98 *S. lineosa*

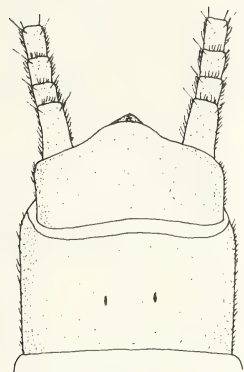
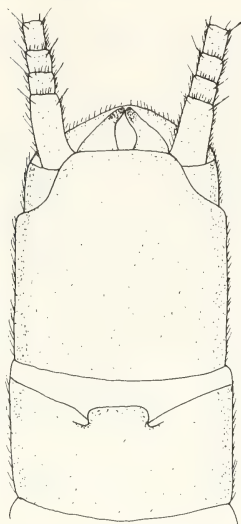
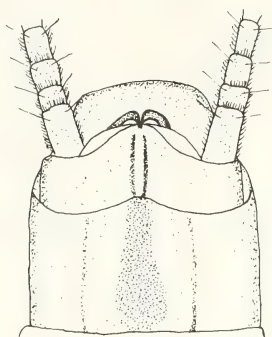
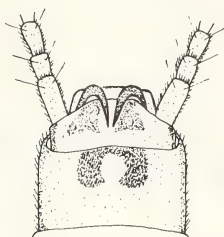
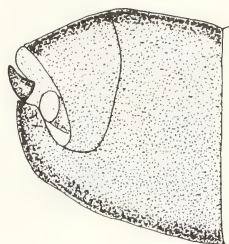
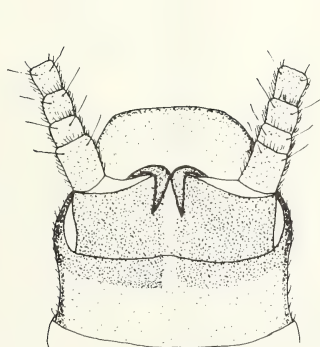
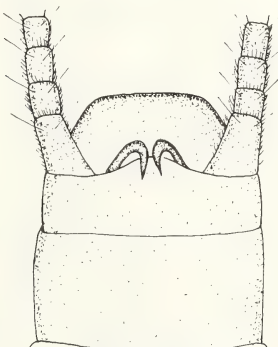
Figures 93 – 98. Genitalia of Chloroperlidae. Fig. 93, *Hastaperla brevis* (male, dorsal); Fig. 94, *Triznaka signata* (male, dorsal); Fig. 95, *Suwallia lineosa* (male, dorsal); Fig. 96, *H. brevis* (female, ventral); Fig. 97, *T. signata* (female, ventral); Fig. 98, *S. lineosa* (female, ventral).

99 *A. abnormis*100 *A. lycorias*101 *H. pacifica*102 *A. lycorias*103 *A. abnormis*104 *H. pacifica*105 *P. media*106 *C. sabulosa*

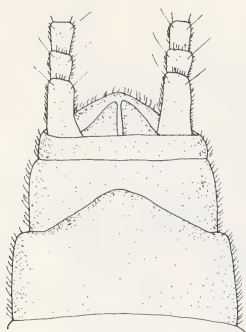
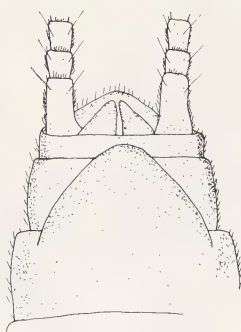
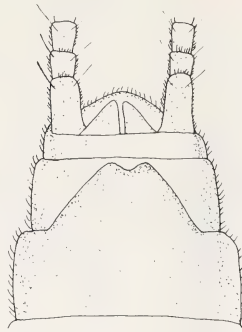
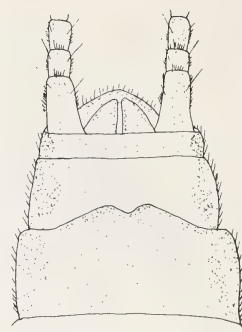
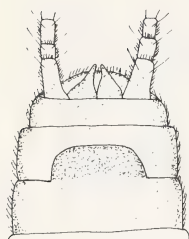
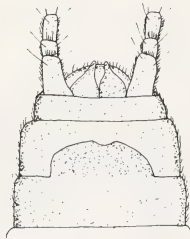
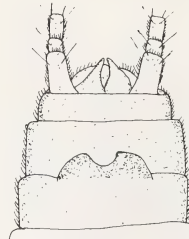
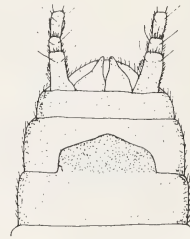
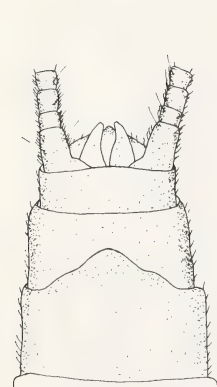
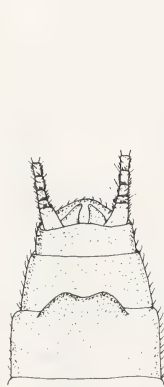
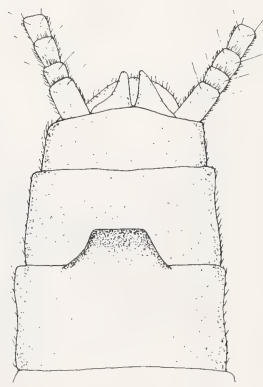
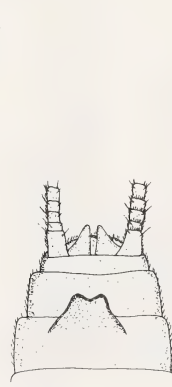
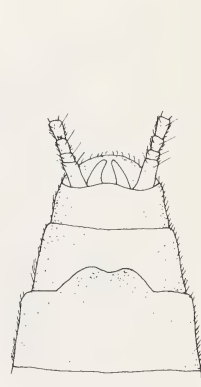
Figures 99 – 106. Genitalia of Perlidae. Fig. 99, *Acroneuria abnormis* (female, ventral); Fig. 100, *A. lycorias* (female, ventral); Fig. 101, *Hesperoperla pacifica* (male, dorsal); Fig. 102, *A. lycorias* (male, dorsal); Fig. 103, *A. abnormis* (male, dorsal); Fig. 104, *H. pacifica* (female, ventral); Fig. 105, *Paragnetina media* (female, ventral); Fig. 106, *Claassenia sabulosa* (female, ventral).

107 *D. bicaudata*108 *D. bicaudata*109 *D. bicaudata*110 *I. colubrinus*111 *I. frontalis*112 *S. parallela*113 *A. compacta*114 *S. parallela*115 *A. compacta*116 *I. colubrinus*

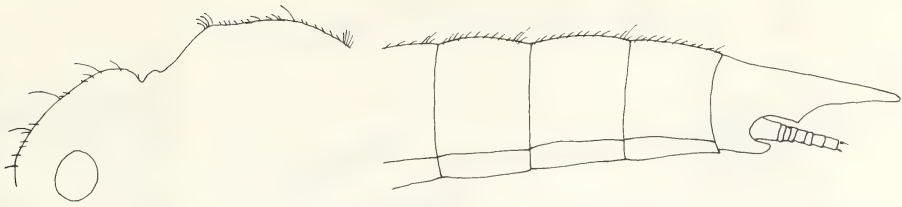
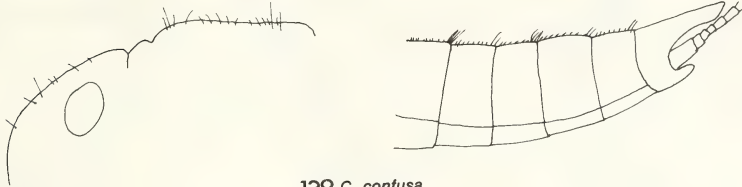
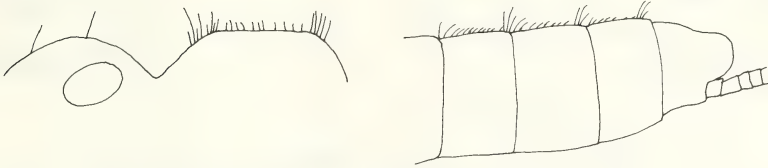
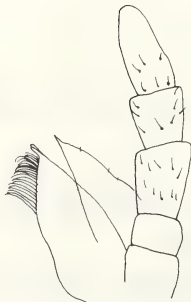
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117 *I. bilineata*118 *I. bilineata*119 *I. transmarina*120 *I. longiseta*121 *I. decolorata*122 *I. patricia*123 *I. petersoni*124 *I. petersoni*

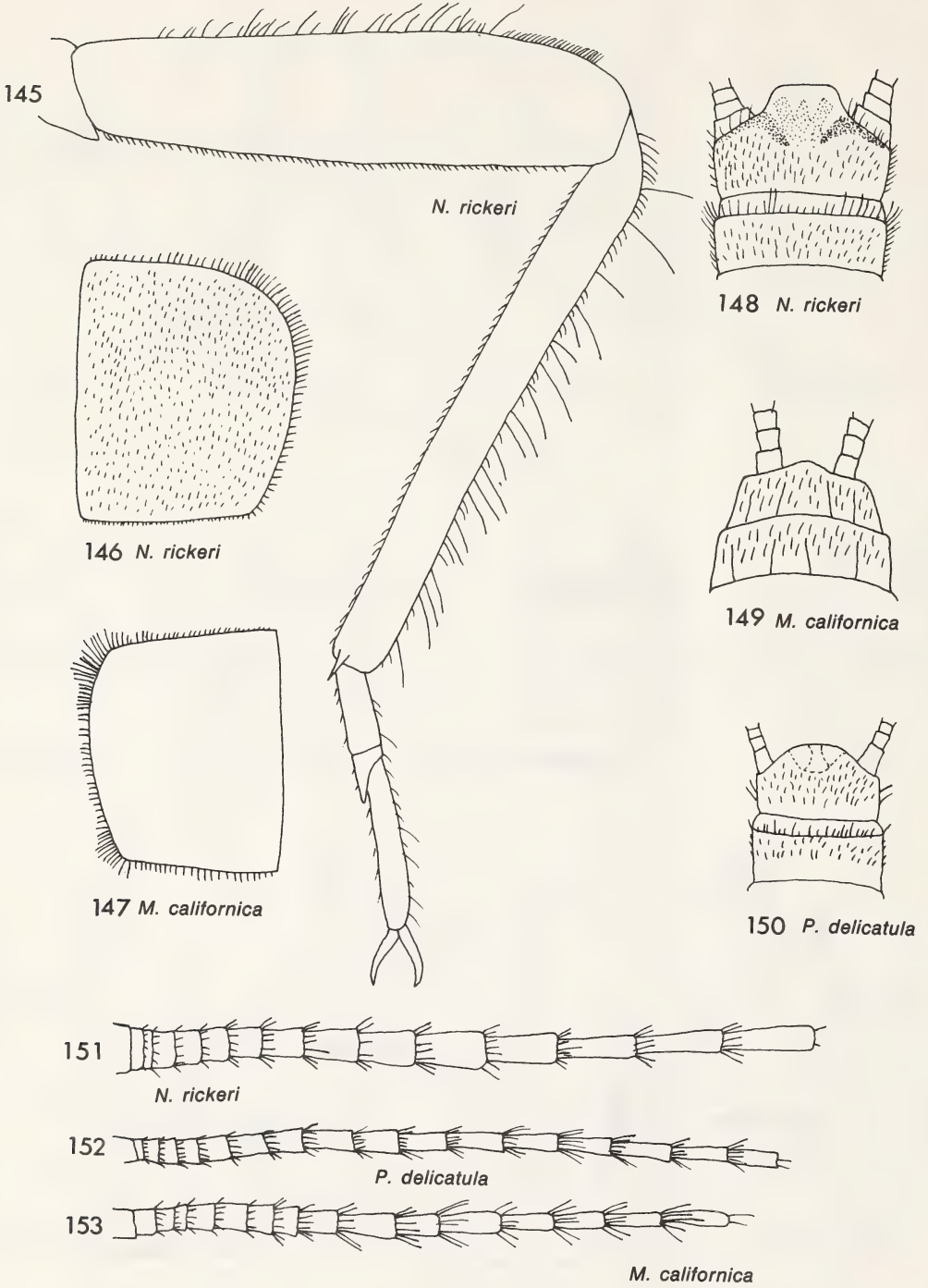
Figures 117 – 124. Male genitalia of Isoperlinae. Fig. 117, *Isoperla bilineata* (dorsal); Fig. 118, *I. bilineata* (ventral); Fig. 119, *I. transmarina* (dorsal); Fig. 120, *I. longiseta* (dorsal); Fig. 121, *I. decolorata* (lateral, cerci removed); Fig. 122, *I. patricia* (dorsal); Fig. 123, *I. petersoni* (dorsal); Fig. 124, Aedeagal process of *I. petersoni* (lateral).

125 *I. bilineata*126 *I. bilineata*127 *I. bilineata*128 *I. bilineata*129 *I. longiseta*130 *I. longiseta*131 *I. longiseta*132 *I. longiseta*133 *I. decolorata*134 *I. petersoni*135 *I. transmarina*136 *I. patricia*137 *I. marlynia*

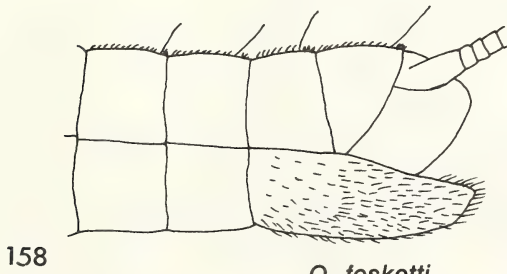
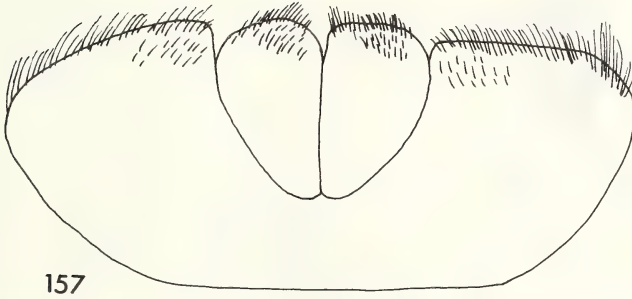
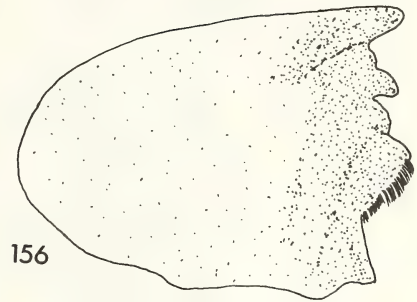
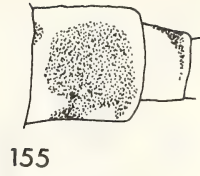
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138 *C. gracilaria*139 *C. confusa*140 *C. coloradensis*141 *C. vernalis*142 *C. confusa*143 *C. gracilaria*144 *C. coloradensis*

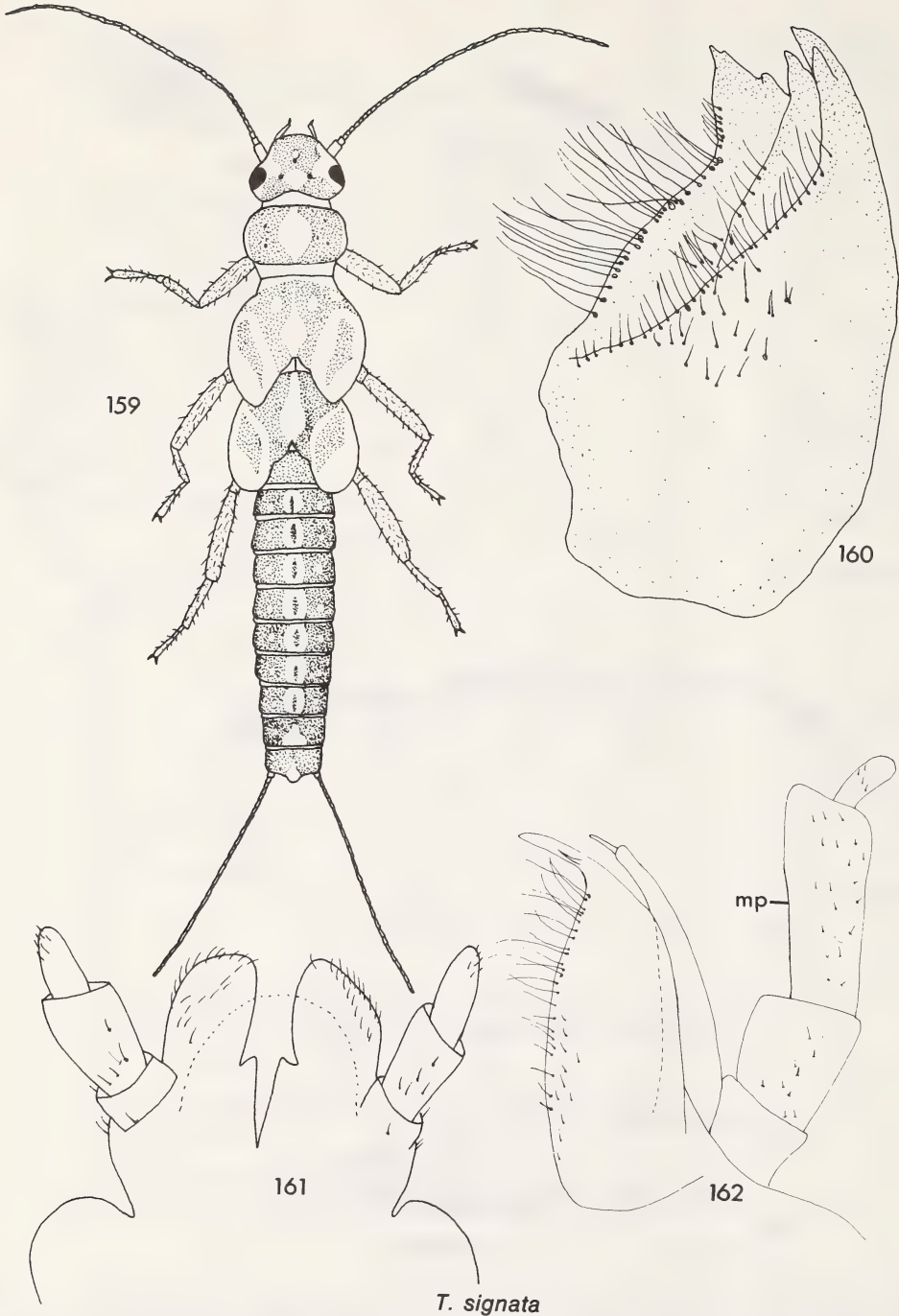
Figures 138 – 144. Nymphal setation and maxillae of Capniidae. Only the setae which can be seen in profile on the top of the head, on the pronotum and on the abdomen have been indicated; the eye is outlined as a point of reference. Fig. 138, *Capnia gracilaria* (male); Fig. 139, *C. confusa* (male); Fig. 140, *C. coloradensis* (female); Fig. 141, Maxilla of *C. vernalis*; Fig. 142, Maxilla of *C. confusa*; Fig. 143, Maxilla of *C. gracilaria*; Fig. 144, Maxilla of *C. coloradensis*.



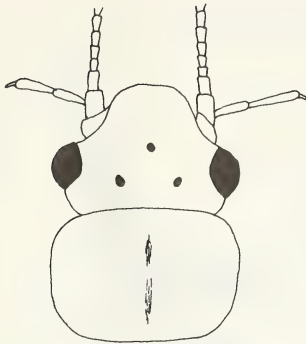
Figures 145 – 153. Setation of Nemouridae nymphs. Fig. 145, Hindleg of *Nemoura rickeri*; Fig. 146, Right half of pronotum of *N. rickeri*; Fig. 147, Left half of pronotum of *Malenka californica*; Fig. 148, Terminal abdominal tergites of *N. rickeri* (male); Fig. 149, Terminal abdominal tergites of *M. californica* (female); Fig. 150, Terminal abdominal tergites of *Podmosta delicatula* (male); Fig. 151, Cerci of *N. rickeri* (lateral); Fig. 152, Cerci of *P. delicatula* (lateral); Fig. 153, Cerci of *M. californica* (lateral).

*O. fosketti*

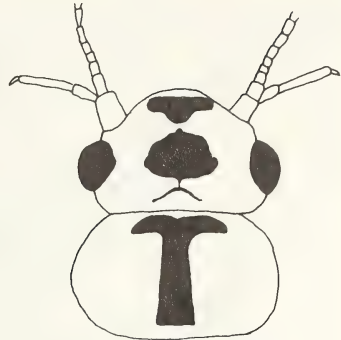
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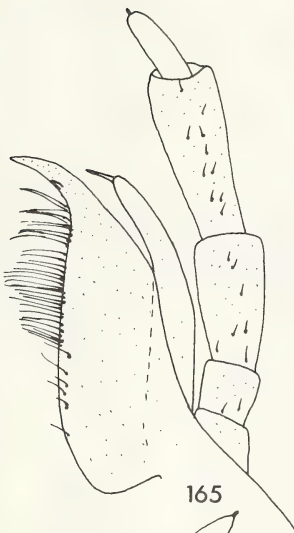
Figures 159 – 162. Nymphal color pattern and mouthparts of *Triznaka signata*. Fig. 159, Mature nymph showing color pattern; Fig. 160, Mandible; Fig. 161, Labium; Fig. 162, Maxilla and maxillary palpus (mp).



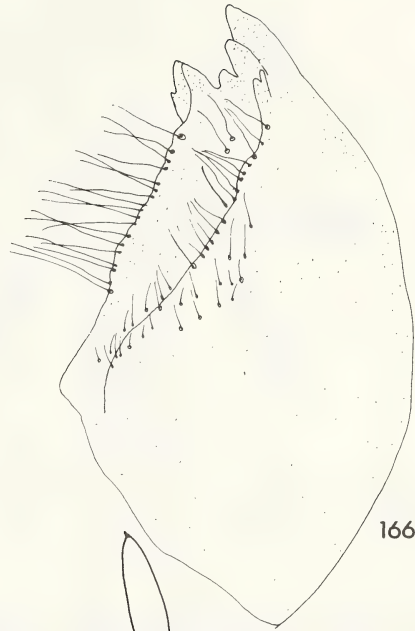
163 *S. lineosa*



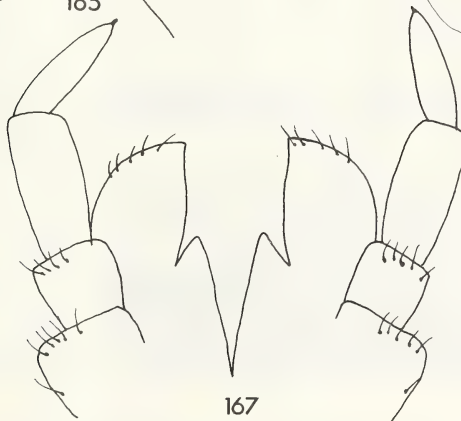
164 *T. signata*



165

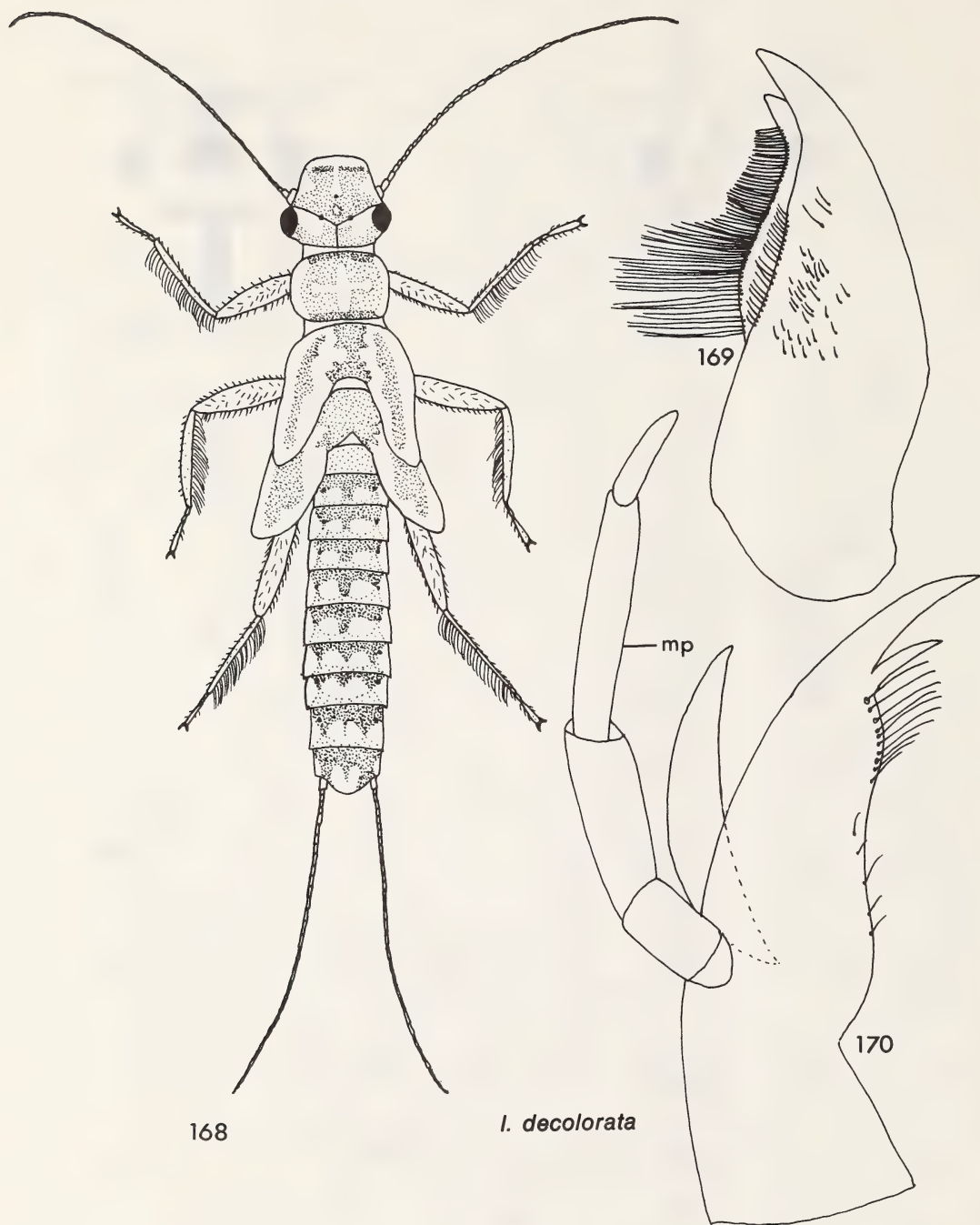


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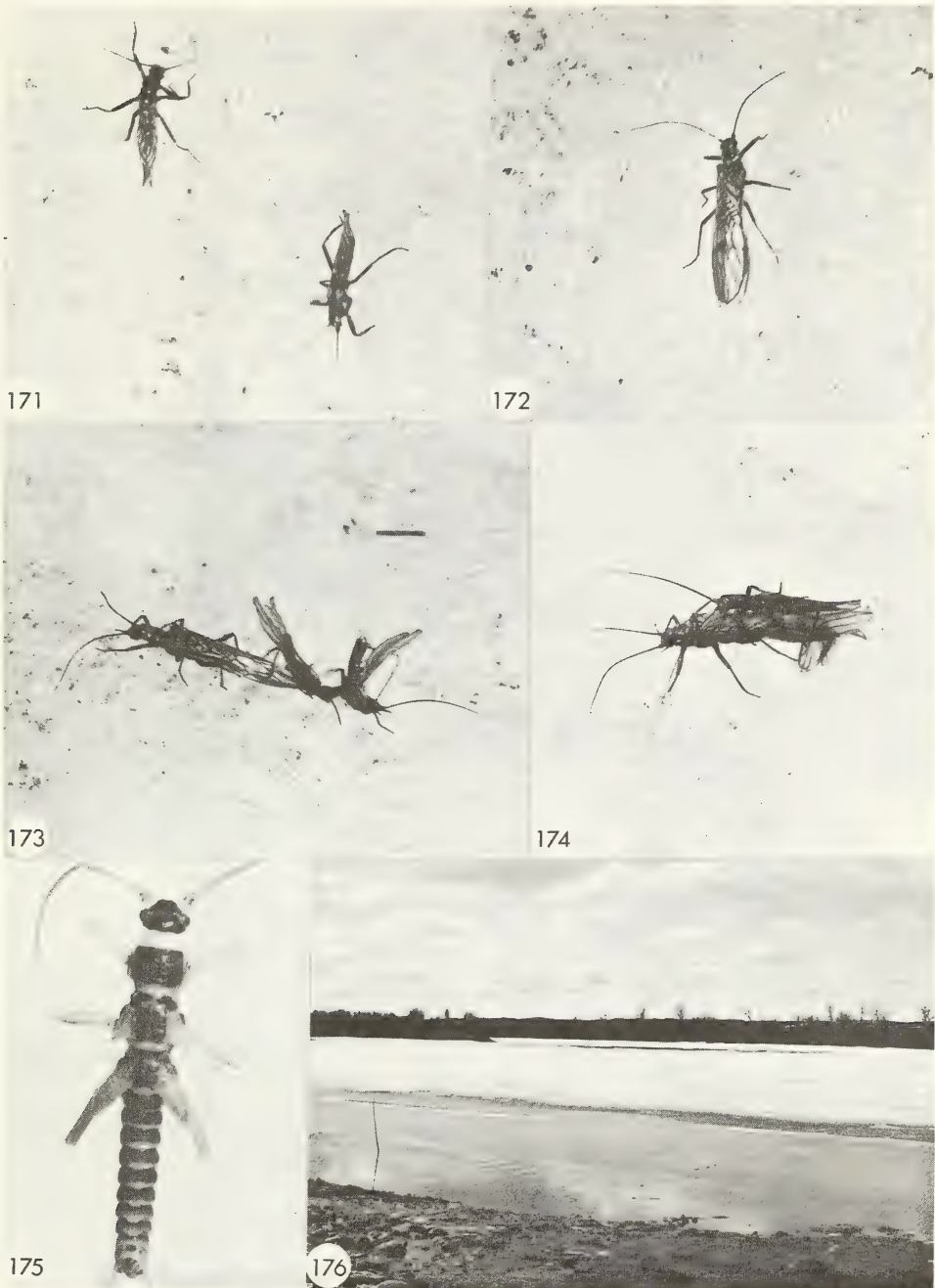


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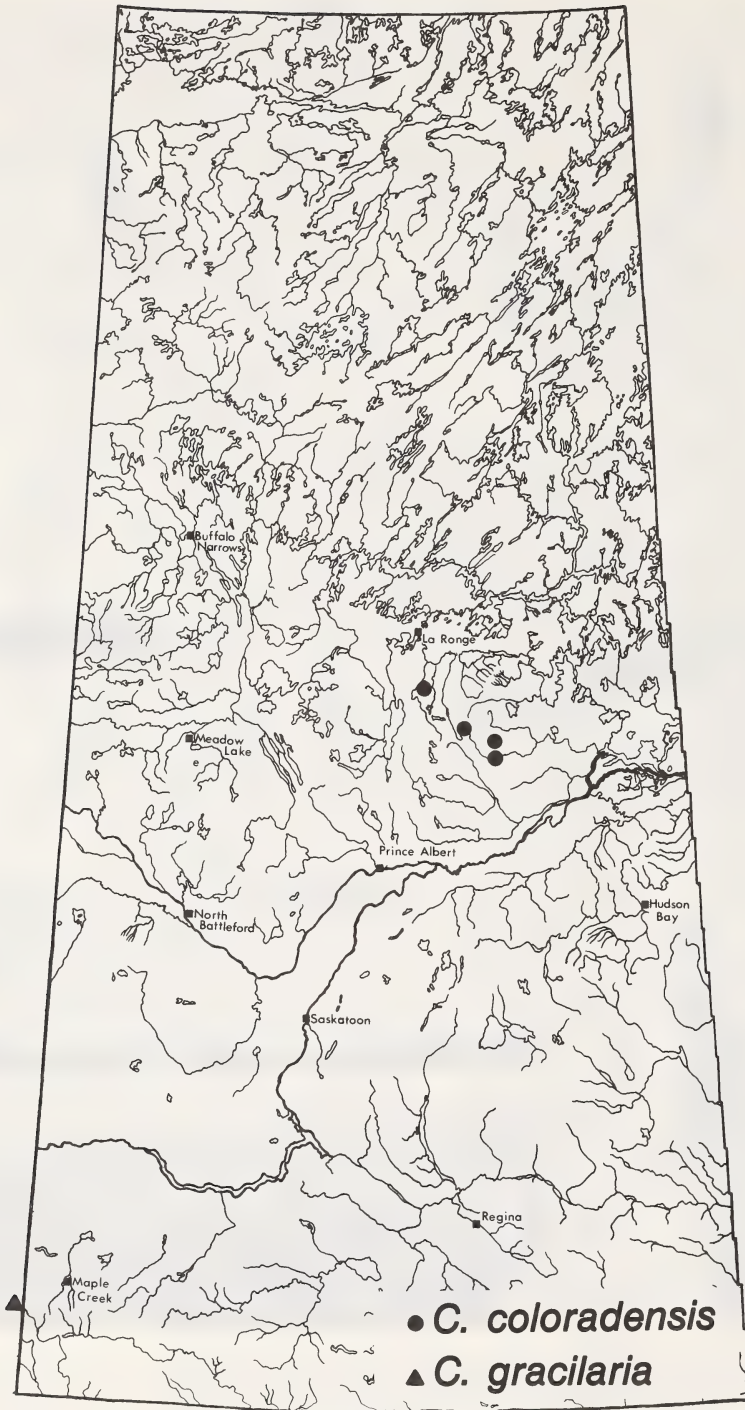
Figures 163 – 167. Adult head patterns and nymphal mouthparts of Chloroperlidae. Fig.163, Head pattern of *Suwallia lineosa*; Fig. 164, Head pattern of *Triznaka signata*; Fig. 165, Maxilla of *S. lineosa*; Fig. 166, Mandible of *S. lineosa*; Fig. 167; Labium of *S. lineosa*.



Figures 168 – 170. Nymphal color pattern and mouthparts of *Isoperla decolorata*. Fig. 168, Mature nymph showing color pattern; Fig. 169, Mandible; Fig. 170, Maxilla with maxillary palpus (mp).

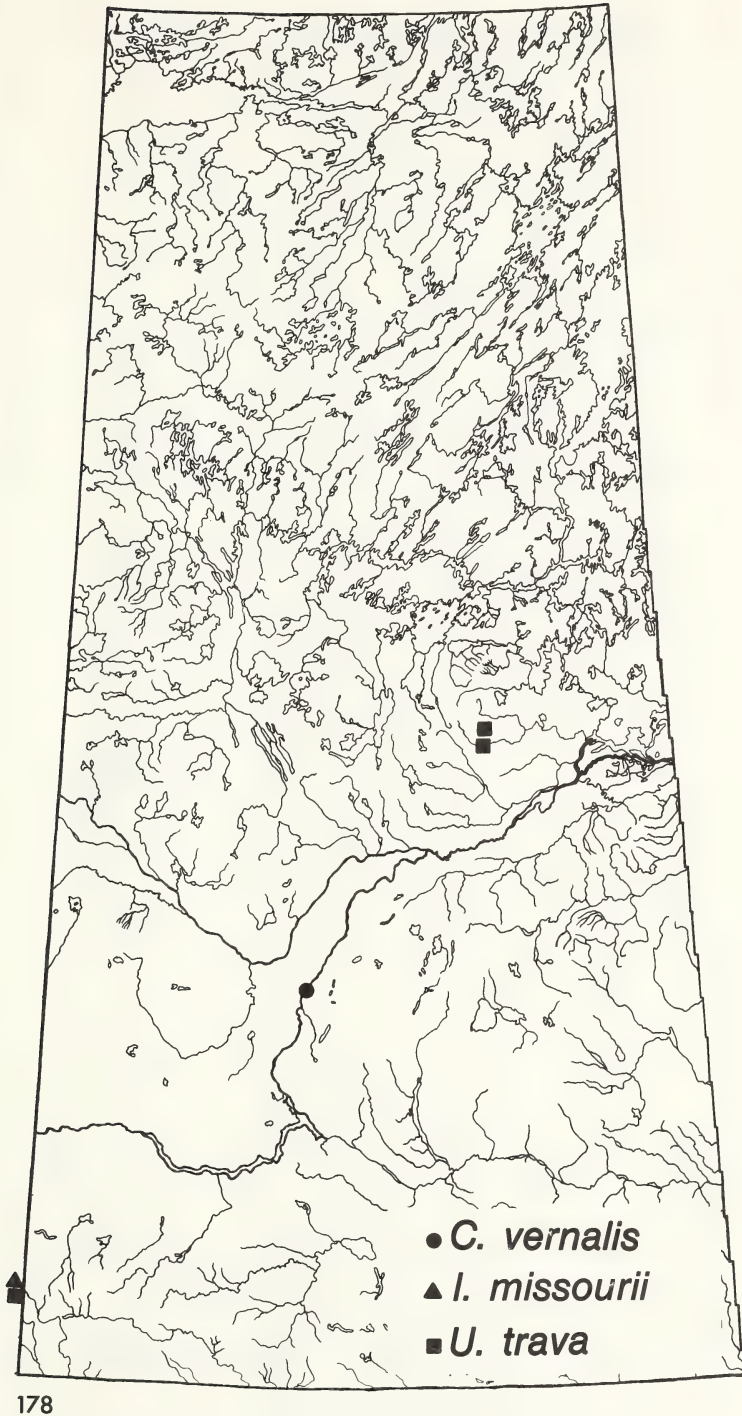


Figures 171 – 176. Adults, nymph and habitat of *Oemopteryx foscetti* under field conditions. Fig. 171, Two males actively searching out females on the snow near the North Saskatchewan River; Fig. 172, Female; Fig. 173, Two males competing for a female; the male nearest the female had begun mating, and upon the arrival of the second male, a struggle ensued until one was driven away; Fig. 174, Mating pair; Fig. 175, Mature male nymph; Fig. 176, North Saskatchewan River partially ice-covered near Borden Bridge (Hwy. 5) at emergence time of *O. foscetti*.



177

Fig. 177, Saskatchewan records for *Capnia coloradensis* and *C. gracilaria*.



178

Fig. 178, Saskatchewan records for *Capnia vernalis*, *Isocapnia missouri* and *Utacapnia trava*.

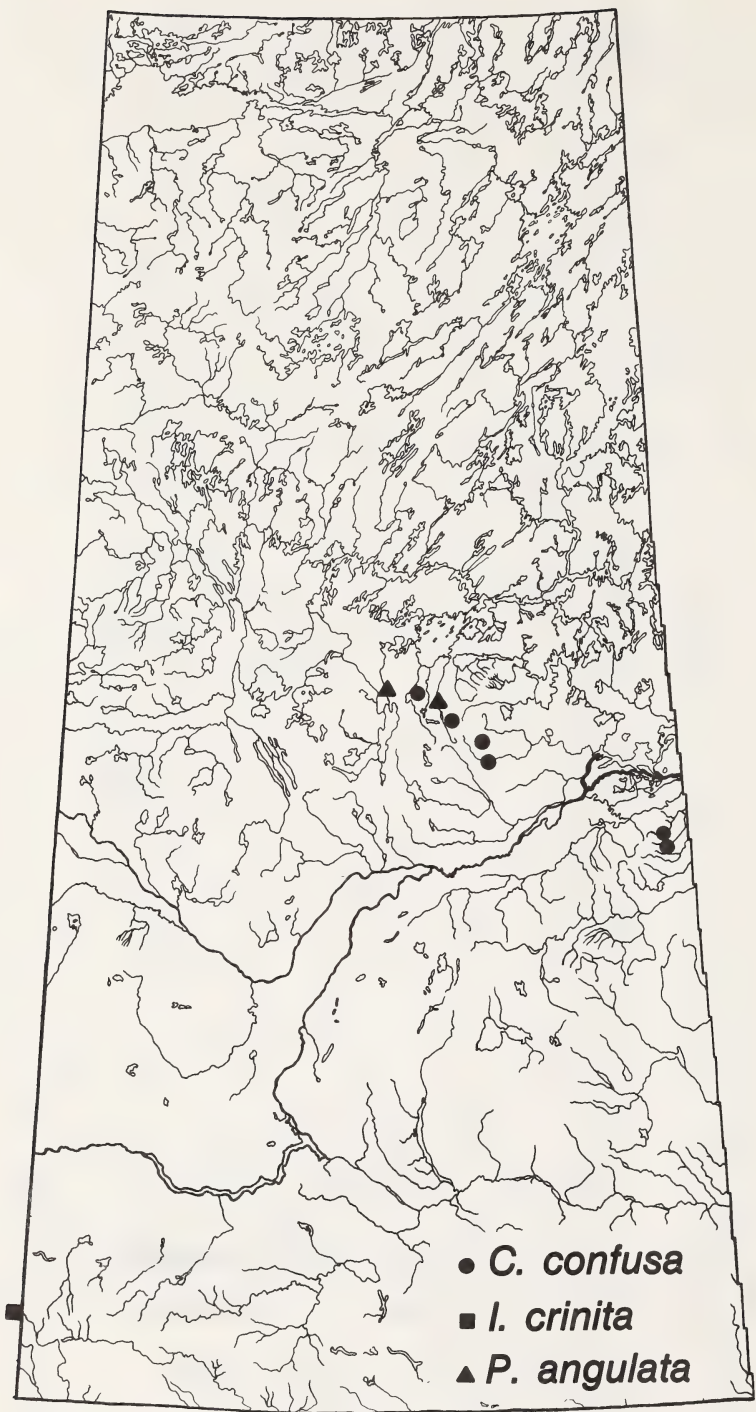
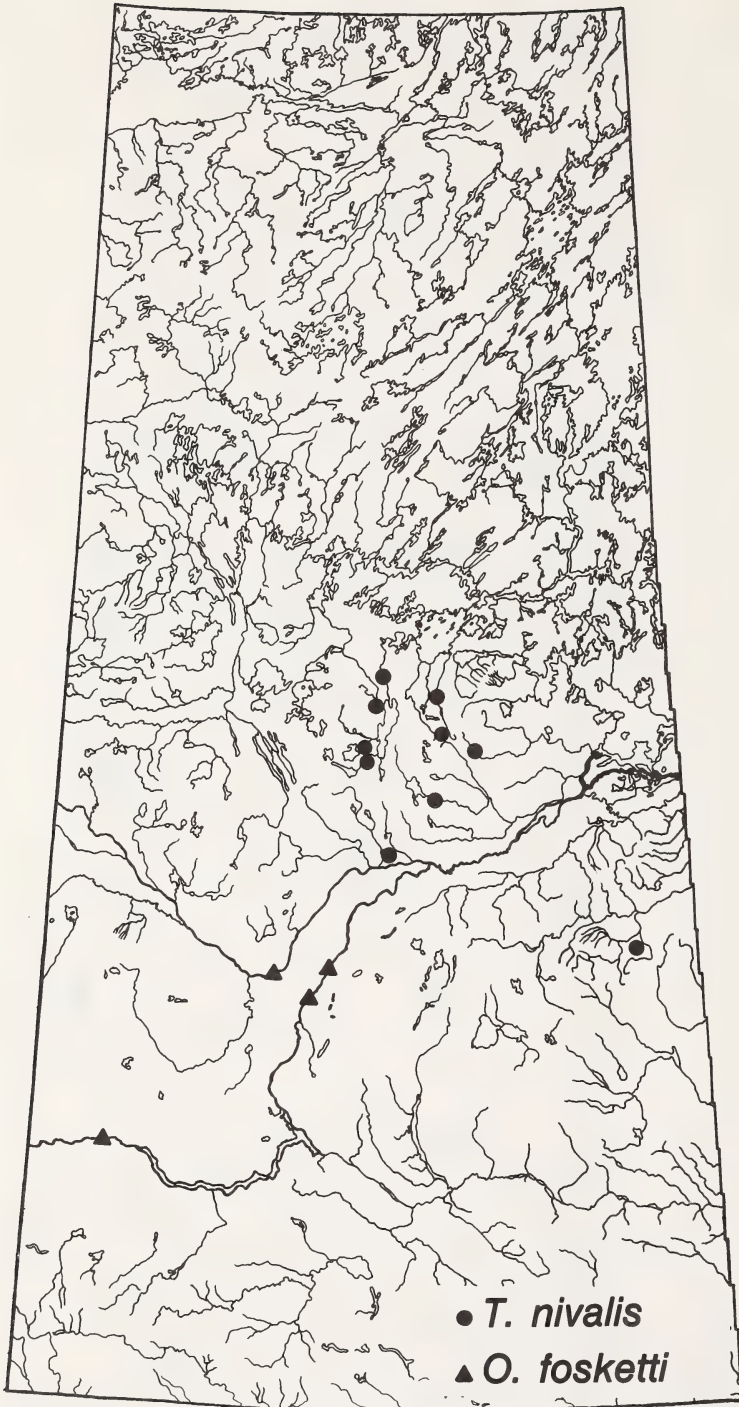


Fig. 179, Saskatchewan records for *Capnia confusa*, *Isocapnia crinita* and *Paracapnia angulata*.



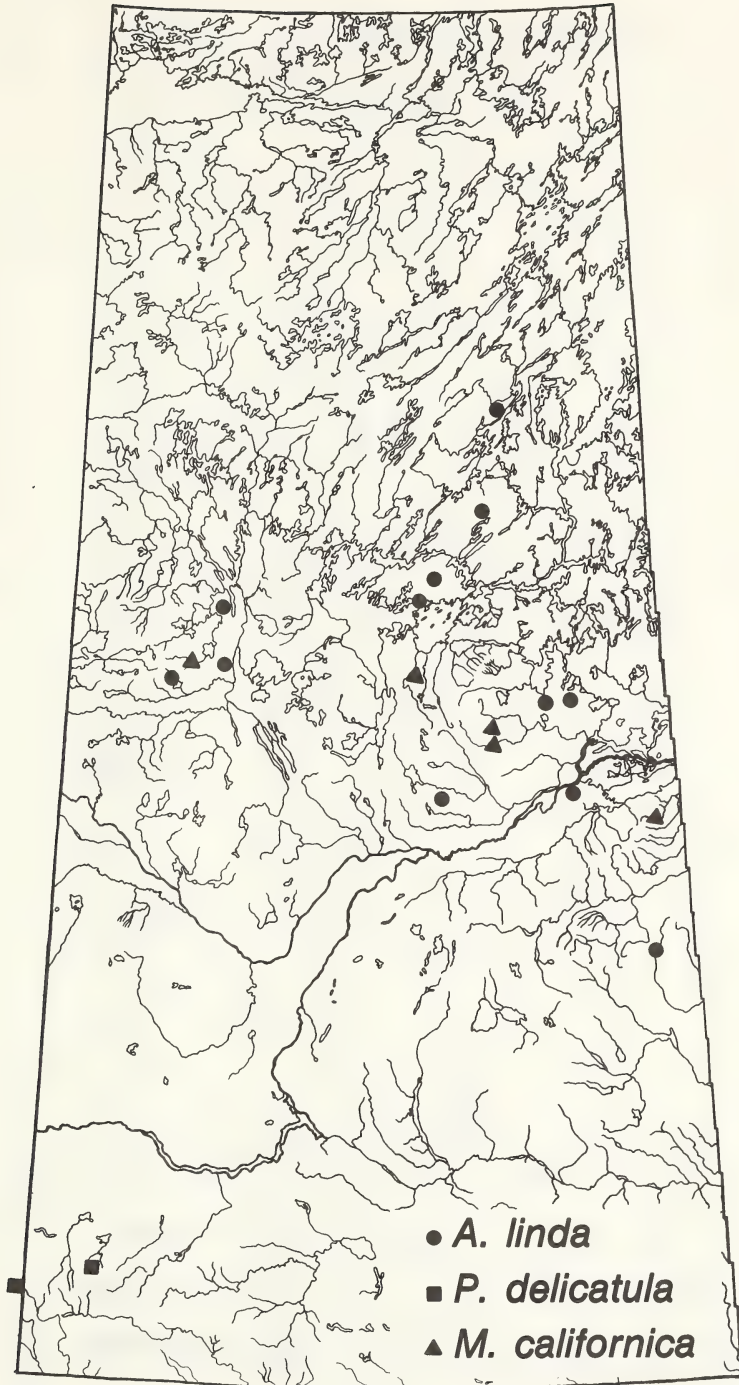
180

Fig. 180, Saskatchewan records for *Pteronarcys dorsata* and *Pteronarcella badia*.



181

Fig. 181, Saskatchewan records for *Taeniopteryx nivalis* and *Oemopteryx foscetti*.

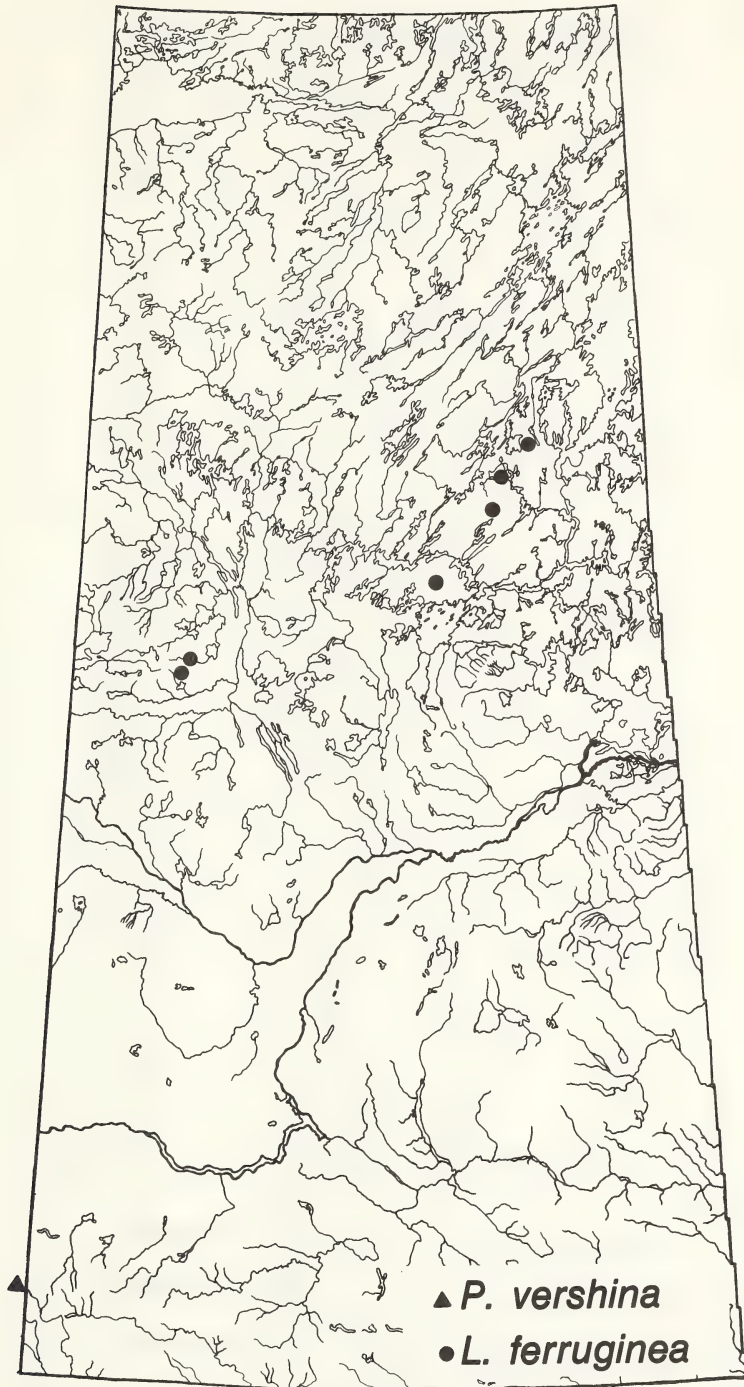


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Fig. 182, Saskatchewan records for *Amphinemura linda*, *Podmosta delicatula* and *Malenka californica*.



Fig. 183, Saskatchewan records for *Nemoura rickeri*, *Zapada cinctipes* and *Shpsa rotunda*.



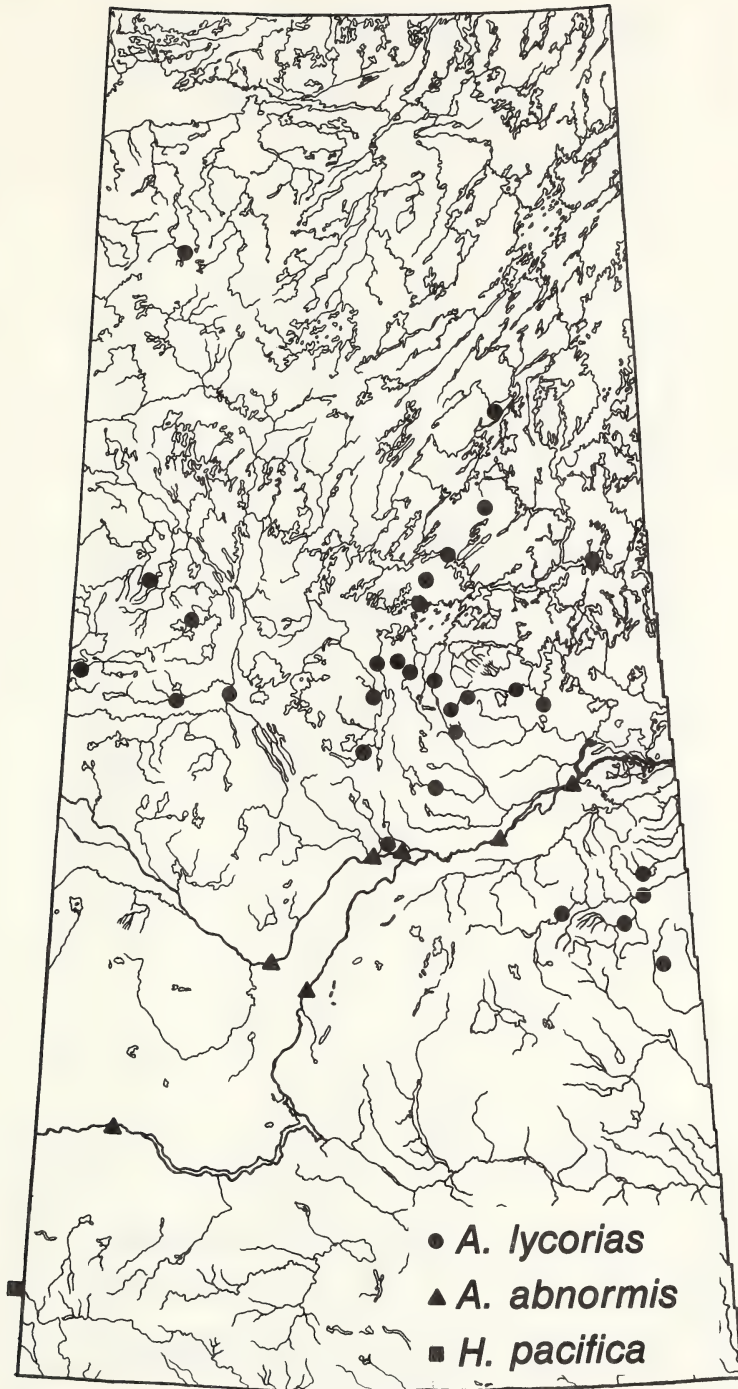
184

Fig. 184, Saskatchewan records for *Paraleuctra vershina* and *Leuctra ferruginea*.



185

Fig. 185, Saskatchewan records for *Hastaperla brevis*, *Suwallia lineosa* and *Triznaka signata*.



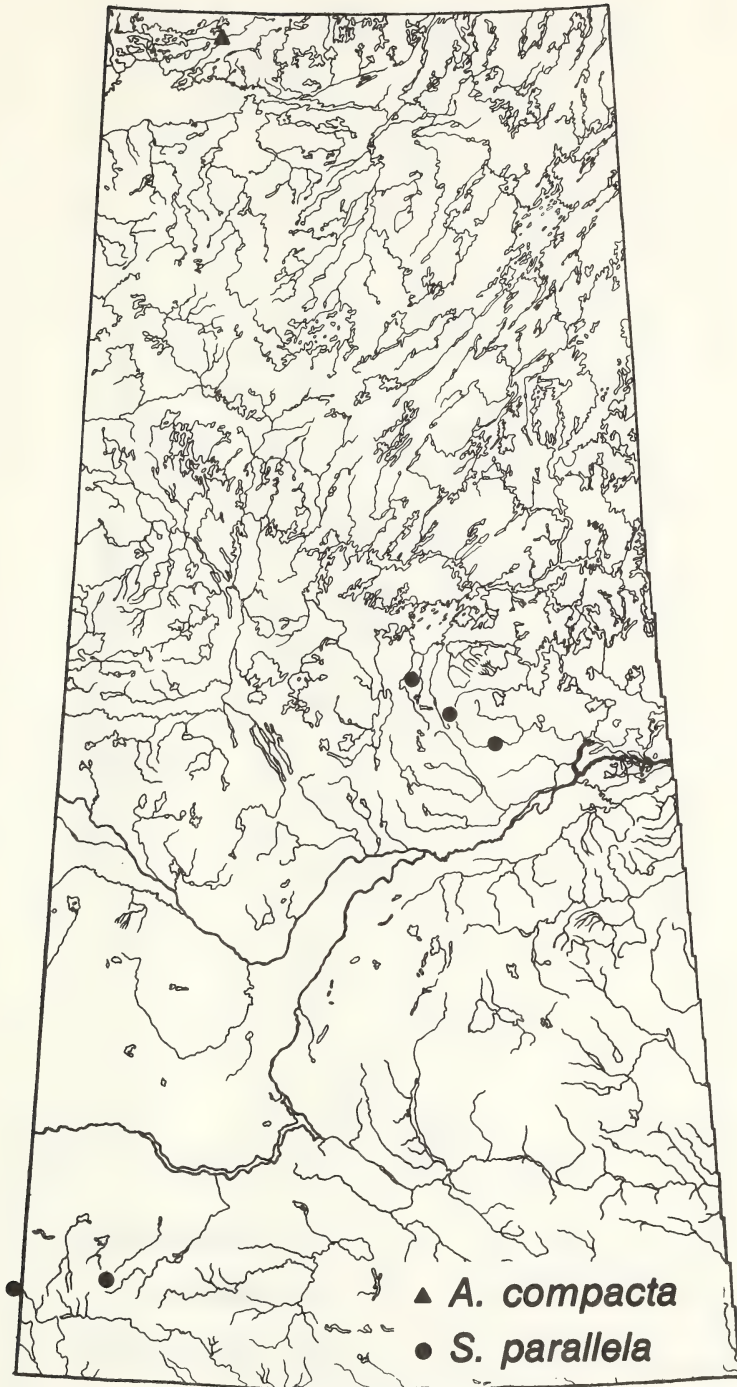
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Fig. 186, Saskatchewan records for *Acroneuria lycorias*, *A. abnormis* and *Hesperoperla pacifica*.



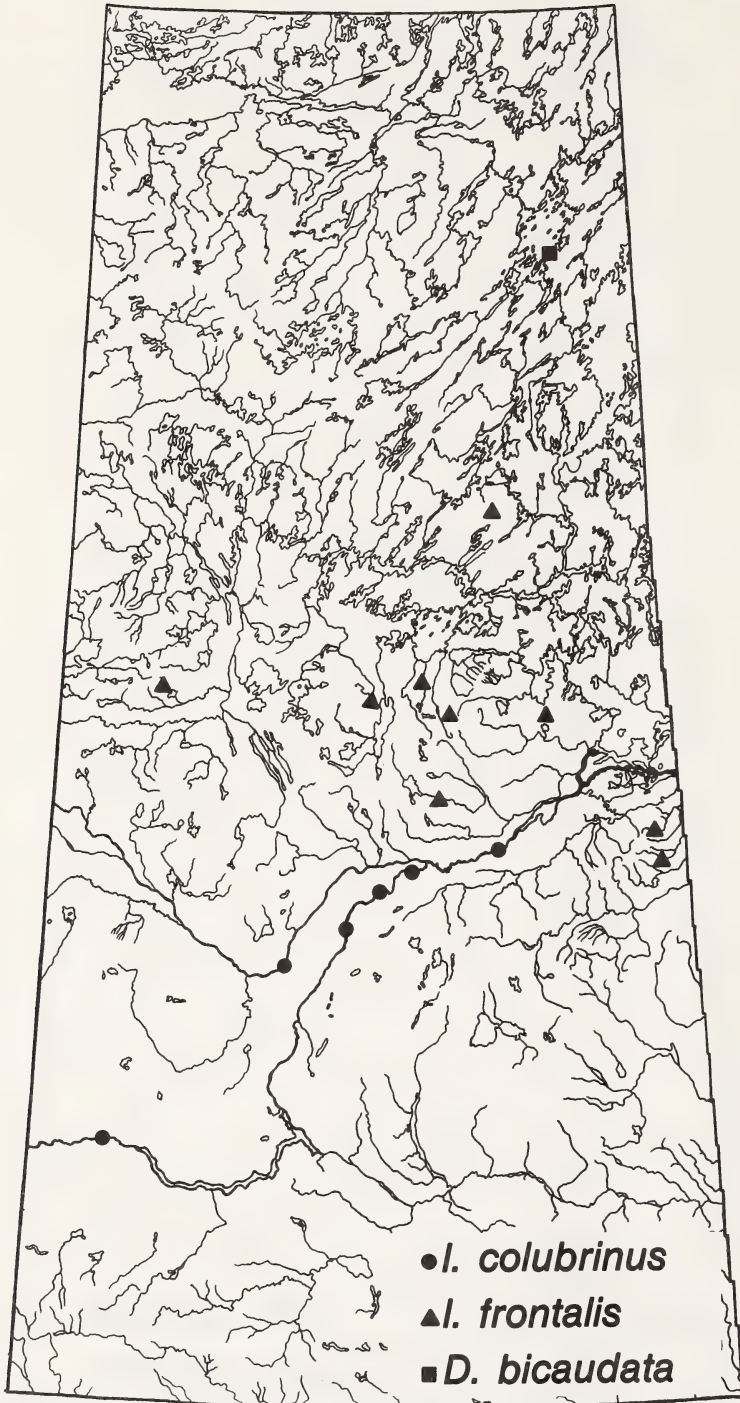
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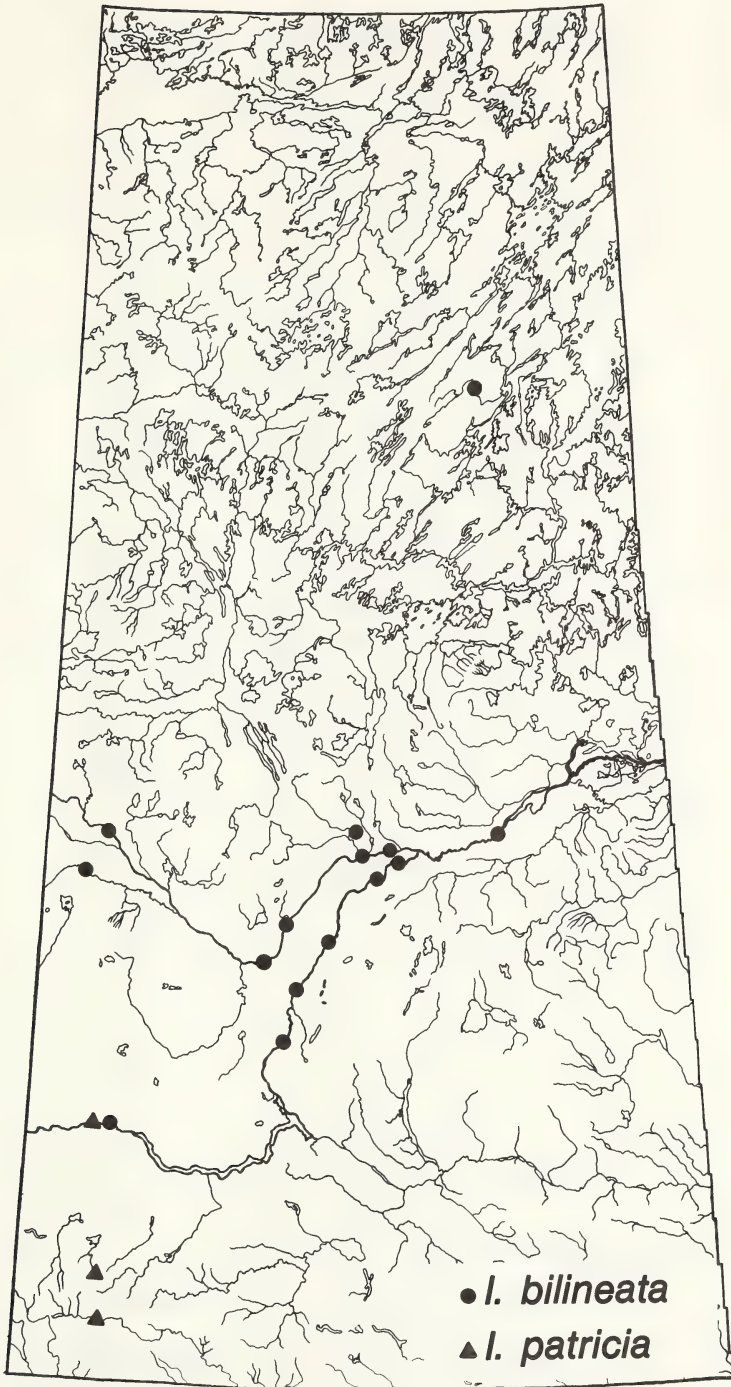
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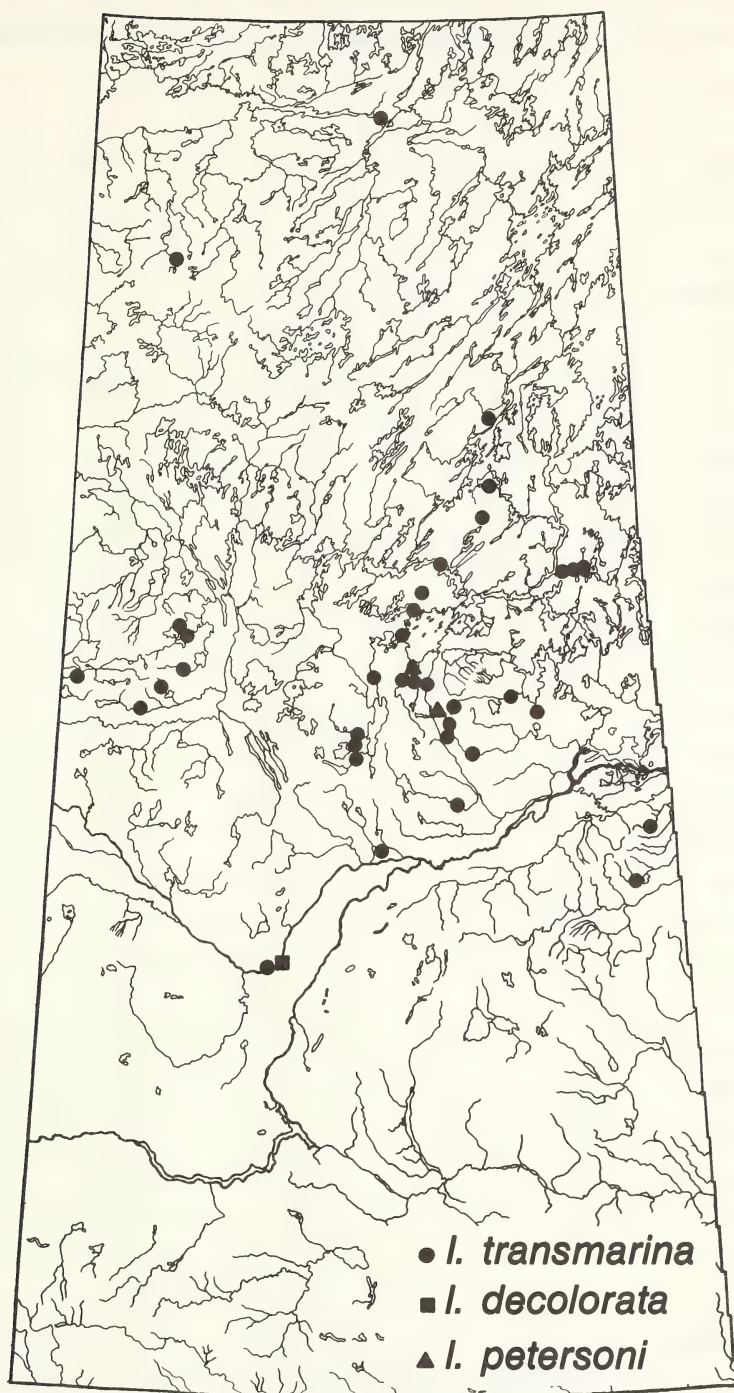
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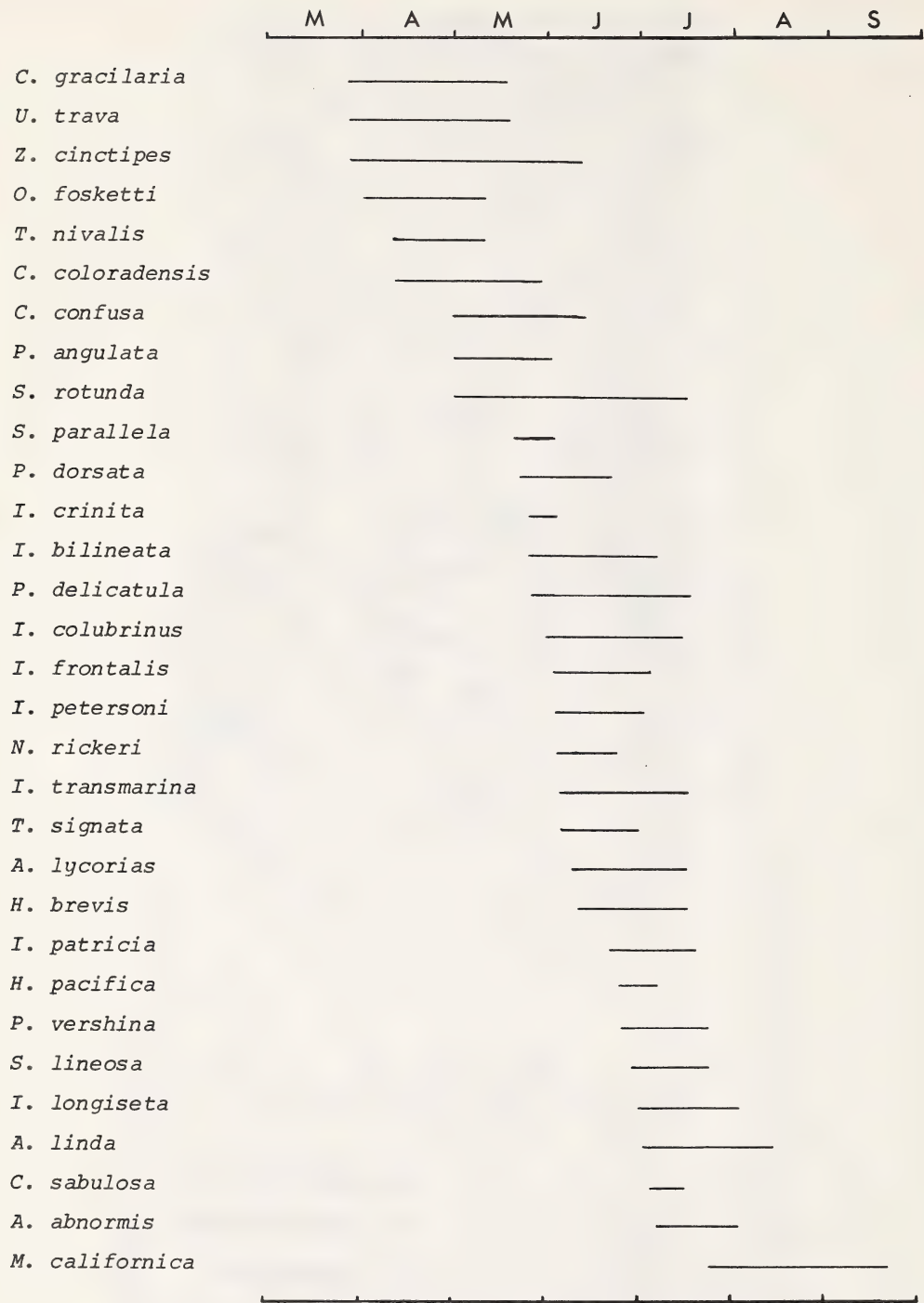


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UPPER OLIGOCENE FOSSIL PUPAE AND LARVAE OF *CHAOBORUS TERTIARIUS*
(VON HEYDEN) (CHAOBORIDAE, DIPTERA) FROM WEST GERMANY

ART BORKENT¹

Department of Entomology
University of Alberta
Edmonton, Alberta, Canada
T6G 2E3

Corrigenda. A. Borkent. *Quaest. Ent.* 14(4): 491–496.

page/line

491 / 44 Change *Culcites tertiaris* von Heyden to *Culicites tertiaris* von Heyden

¹Present Address: Biosystematics Research Institute, Research Branch, Agriculture Canada,
Ottawa, Ontario, Canada K1A 0C6.

Editorial – To Compute or Not Compute

There have been many attempts to cast Shakespeare's plays in 20th century format, some successful, others not. Recently, I have read various attempts at rewriting, in modern English, Hamlet's soliloquy "To be or not to be, that is the question.....". One such attempt (here somewhat modified) was: "To compute or not compute, that is the go/no-go decision".

The quotation is appropriate to *Quaestiones Entomologicae*, as the text for this, and I hope for other issues, was and will be produced using a computer textformatting program. Why change from our time-tested methods of production? Proofs and satisfactory copy for *Quaestiones Entomologicae* were previously produced on a special, highly sophisticated typewriter. This machine has been gradually wearing out and the cost of replacement has proved to be prohibitive. As textformatting programs were available through an existing computer facility at the University of Alberta, it seemed logical to make use of them, if we were to continue publication of *Quaestiones Entomologicae*.

The Michigan Terminal System is now used for typing manuscripts. Text is typed using the editor mode and proofs are run off on a computer line printer. When all corrections are made, the text is transferred to a magnetic tape and sent to the printers where a phototypesetter produces final copy for printing.

Use of textformatting programs offers certain advantages over the more traditional method of producing *Quaestiones Entomologicae*. One advantage is that indexing can be done at the same time as the text is being typed into the computer terminal. Producing the index is now easy and fast whereas it was a time consuming and onerous task.

The decision to switch to textformatting for production of *Quaestiones Entomologicae* was taken by the editor, George E. Ball, about one year ago. When George left on sabbatical leave last year, he persuaded me to be Acting Editor until his return later this year. I was horrified to discover that I would have to oversee production of the first issue of *Quaestiones Entomologicae* produced by the new method. Fortunately for me, all textformatting and associated problems have been handled by Twyla Gibson who has been Publication Assistant of *Quaestiones Entomologicae* for the past year. To her I owe a great deal of thanks. Her attention to detail has made my job as Acting Editor much easier. Also, a special tribute and thank you to D. Reinhart of Printing Services, University of Alberta, for designing the textformatting layout that we are using for *Quaestiones Entomologicae*.

The quality of an editor's life is further enhanced by those willing to review manuscripts and I thank the following for reviewing papers in Volume 14 and this issue of Volume 15: G.E. Ball, W.G. Evans, L.H. Herman, J. Kukalova-Peck, A.P. Nimmo and D.R. Whitehead. Thanks also to H. Goulet for translating the abstracts into French.

Unfortunately, I have to announce an increase in page charges. We have always held these charges as low as possible and they have been \$11.00 per page for the past five years. However, increases in production and printing costs now require a charge of \$15.00 per page. Costs of reprints will be \$3.00 per page per 100 copies.

Until George Ball resumes editorship, I intend to maintain the standards set by him. Some people no doubt are natural editors, others like me have the responsibility thrust upon them. I have much to learn. I certainly have a greater appreciation now of the steps involved in getting a manuscript published. In fact all who publish should serve time as an editor as it would improve the quality of their subsequently submitted manuscripts.

Douglas A. Craig

Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for comprehensive accounts of entomological research of greater than average length. Page charges are normally levied, the rate determined by printer's charges. For example, for the period 1968 - 1972, the charge was \$5.00 per page; for 1973, \$5.30; for 1974, \$7.00. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the Style Manual for Biological Journals, published by the American Institute of Biological Sciences, Second Edition, 1964, except that titles of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. All manuscripts will be reviewed by referees.

Abstracts of not more than 500 words are required: one in English, and one in another language, preferably French.

Tables must be not more than $7\frac{3}{4} \times 4\frac{3}{4}$ inches (19.7×12.1 cm), and plates and figures not more than $8\frac{1}{2} \times 6$ inches (21.6×15.2 cm). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries, and individuals, \$8.00 per volume of 4 issues, normally appearing at quarterly intervals; single issues \$3.00. Back volumes I-X are available at \$6.00 per volume, single issues at \$1.50 per copy. Back volumes 11-15 will be available at \$10.00 per volume, single issues \$3.00 per copy. These prices are subject to change as required by inflationary pressure on the value of money.

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The Editor, *Quaestiones Entomologicae*,
Department of Entomology,
University of Alberta
Edmonton, Alberta, Canada T6G 2E3

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FRONTISPIECE



Chaoborus trivittatus adult male.

SYSTEMATICS AND BIONOMICS OF THE SPECIES OF THE SUBGENUS
SCHADONOPHASMA DYAR AND SHANNON (*CHAOBORUS*, CHAOBORIDAE, DIPTERA)¹

ART BORKENT²

Department of Entomology

University of Alberta

Edmonton, Alberta, Canada

T6G 2E3

Quaestiones Entomologicae

15: 122-255 1979

Study of structure, intraspecific variation, life cycles and bionomic features suggests the presence of three species of the subgenus Schadonophasma. Chaoborus trivittatus (Loew) and Chaoborus cooki Saether are restricted to North America while Chaoborus nyblaei (Zetterstedt) is known only from Fennoscandia. Chaoborus brunskilli Saether and Chaoborus knabi (Dyar) are conspecific with C. trivittatus

All stages of each species were studied except first, second and third larval instars of C. nyblaei which are unknown. Eggs of C. cooki and C. nyblaei, unlike those of C. trivittatus, exhibit a thickened exochorion. C. cooki eggs are laid in a spherical mass with little gelatinous matrix while those of C. trivittatus are laid in a spiral arrangement in a disc of gelatinous matrix. First instar larvae of C. cooki possess a more pronounced egg burster than do those of C. trivittatus. All other stages can be distinguished only by using a combination of characters. A compound character index is provided for separation of fourth instar larvae of C. trivittatus and C. cooki and was used to test possibilities of conspecificity of these two species. Male adults can be identified by the shape of the penis valves and a ratio of the length of two wing veins.

The thickened exochorion of eggs of C. cooki, and probably C. nyblaei, is an adaptation to overwintering as eggs in temporary ponds. C. cooki is univoltine. C. trivittatus immatures occur mostly in permanent lentic habitats where this species overwinters as a fourth instar larva. This species may be uni- or multivoltine or have a two year life cycle.

Behavioural differences are evident between C. trivittatus and C. cooki. Only C. cooki larvae are capable of ingesting ostracods. Male adults of C. trivittatus form large swarms. Adult females are the main dispersing agent of C. trivittatus while limited evidence for C. cooki suggests that both sexes of this species disperse. Under laboratory conditions C. trivittatus male adults live up to seven to eight days and female adults up to twelve days.

The pattern of intraspecific variation indicates that some of the variation of fourth instar larvae is due to sex-associated, age-related and geographical variation. Geographical variation of characters of fourth instar larvae and geographical distribution of C. trivittatus indicates that this species was present in the Beringian refugium and those refugia south of the continental ice sheet during the Wisconsin glaciation.

A reconstructed phylogeny of some Chaoborus species is provided. The subgenera Schadonophasma and Chaoborus s. str. are both monophyletic and are sister groups. An upper Oligocene Chaoborus fossil indicates the minimum age of the speciation events which gave rise to the ancestor of these two groups, to be 25 million years.

¹Based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at the University of Alberta, Edmonton, Canada.

²Present address: c/o D.M. Wood, Biosystematics Research Institute, Research Branch, Agriculture Canada, Ottawa, Ontario, Canada K1A 0C6

A reconstructed phylogeny of Schadonophasma species indicates that C. cooki and C. nyblaei are more closely related to each other than either is to C. trivittatus. Zoogeographic considerations suggest two possible hypotheses for the origin of these species. The first invokes allopatric speciation between the Nearctic and Palearctic regions producing C. trivittatus and the ancestor of C. cooki and C. nyblaei. Subsequent geographical isolation of populations of the latter lineage produced C. cooki and C. nyblaei. The second hypothesis differs in proposing that the C. cooki-nyblaei lineage arose in sympatry with C. trivittatus from individuals of a C. trivittatus-like ancestor that involved an overwintering egg stage which allowed exploitation of temporary habitats. A model for the development of reproductive isolation in sympatry suggests the occurrence of a mutation resulting in a diapausing egg in the ancestral population. Through temporal disjunction of mating periods, homogamic mating, complete selection against overwintering larvae in temporary ponds and overwintering eggs in permanent ponds, the two lineages which gave rise to C. trivittatus and the ancestor of C. cooki-nyblaei became genetically isolated.

L'étude de la morphologie, des variations intraspécifiques, des cycles vitaux et de l'histoire naturelle suggère que le sous-genre Schadonophasma consiste en trois espèces. Chaoborus trivittatus (Loew) et Chaoborus cooki Saether ne se rencontrent qu'en Amérique du Nord, alors que Chaoborus nyblaei (Zetterstedt) n'est connu que de la Scandinavie. Je considère Chaoborus brunskilli Saether et Chaoborus knabi (Dyar) comme appartenant à C. trivittatus.

J'ai étudié tous les stades de chaque espèce, sauf les premier, deuxième et troisième âges larvaires de C. nyblaei, qui sont inconnus. Les oeufs de C. cooki et de C. nyblaei, contrairement à ceux de C. trivittatus, ont un exochorion épais. Les oeufs de C. cooki sont déposés en une masse sphérique entourée d'un peu de matière gélatineuse, alors que ceux de C. trivittatus sont déposés en spirale dans un disque de matière gélatineuse. Les larves du premier âge de C. cooki ont un ovorupteur plus prononcé que celles de C. trivittatus. Tous les autres stades ne peuvent être distingués que par des combinaisons de caractères. Un index, défini par de telles combinaisons, permet de séparer les larves du quatrième âge de C. trivittatus et de C. cooki, et a été utilisé pour vérifier que ces deux espèces étaient bien distinctes l'une de l'autre. Les adultes mâles peuvent être identifiés par la forme des valves de l'édéage et par un rapport entre les longueurs de deux des nervures alaires.

L'exochorion épais des oeufs de C. cooki, et probablement de C. nyblaei, est une adaptation pour l'hibernation au stade d'oeuf dans les étangs temporaires. C. cooki n'a qu'une seule génération par année. Les immatures de C. trivittatus se rencontrent surtout dans les étangs permanents où les larves du quatrième âge hibernent. Cette espèce peut avoir une ou plusieurs générations par année, ou avoir un cycle vital de deux ans.

Il y a plusieurs différences entre le comportement de C. trivittatus et celui de C. cooki. Seules les larves de C. cooki peuvent se nourrir d'ostracodes. Les adultes mâles de C. trivittatus s'assemblent en grands essais. Les adultes femelles constituent le principal agent de dispersion de C. trivittatus, alors que chez C. cooki, il semblerait que les deux sexes participent à la dispersion. En laboratoire, les mâles de C. trivittatus vivent jusqu'à sept ou huit jours, alors que les femelles vivent jusqu'à douze jours.

La variabilité intraspécifique chez les larves du quatrième âge serait reliée au sexe et à l'âge, ainsi qu'à des facteurs géographiques. La variation géographique des caractères du quatrième âge larvaire et la répartition géographique de C. trivittatus indiquent que cette espèce était présente dans le refuge de Bering, ainsi que dans le refuge situé au sud de la calotte glaciaire continentale durant la glaciation du Wisconsin.

J'ai reconstruit la phylogénie de quelques espèces de Chaoborus. Les sous-genres Schadonophasma et Chaoborus s. str. sont monophylétiques et apparentés. Un fossile de Chaoborus datant de l'Oligocène supérieur suggère que le processus de spéciation ayant produit l'ancêtre de ces deux sous-genres a eu lieu il y a au moins 25 millions d'années.

Une reconstruction de la phylogénie des espèces de Schadonophasma montre que C. cooki et C. nyblaei sont plus étroitement apparentés l'un à l'autre que chacun d'eux ne l'est à C. trivittatus. Une étude biogéographique suggère deux hypothèses quant à l'origine de ces espèces. La première, basée sur le principe d'évolution allopatrique, suggère que C. trivittatus et l'ancêtre de C. cooki-nyblaei résultèrent d'une séparation de la population de leur ancêtre commun en deux populations, une néarctique et une paléarctique. Une séparation géographique subséquente de la population paléarctique aurait produit C. cooki et C. nyblaei. Suivant la seconde hypothèse, la lignée C. cooki-nyblaei aurait évolué en sympatrie avec C. trivittatus, et serait dérivée d'individus semblables à l'ancêtre de C. trivittatus, mais hibernant au stade d'oeuf, cette dernière adaptation ayant permis l'exploitation des habitats temporaires. J'explique l'évolution de l'isolement reproducteur entre ces deux lignées sympatriques comme suit: une mutation aurait introduit la diapause au stade d'oeuf dans la population ancestrale; grâce à une séparation temporelle des périodes reproductrices, permettant ainsi des accouplements homogamiques, et grâce à une sélection totale contre l'hibernation à l'état larvaire dans les étangs temporaires d'une part, et contre l'hibernation à l'état d'oeuf dans les étangs permanents d'autre part, les deux lignées qui produisirent C. trivittatus et l'ancêtre de C. cooki-nyblaei devinrent génétiquement isolées.

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INTRODUCTION

For systematists interested in understanding the intraspecific and interspecific variation of species, a frequent concern is the investigation of species which do not exhibit discrete morphological characteristics allowing identification of individuals. This study is partially an investigation of such a problem within the genus *Chaoborus* Lichtenstein. I first recognized that it was difficult to separate species of the subgenus *Schadonophasma* Dyar and Shannon, while attempting to identify fourth instar larvae, pupae and adults using Saether's (1972) key. Some specimens exhibited combinations of characters from different species, as delimited by Saether (1970, 1972). I therefore undertook a reinterpretation of variation exhibited by members of this subgenus through examination of the structural and bionomic features of eggs, all stages of larvae, pupae and adults.

Although *Chaoborus* is assigned species that have marked variation and show slight morphological differences between species, few studies have attempted to precisely interpret this variation. Saether (1967) showed that the characters previously thought to separate *Chaoborus flavicans* (Meigen) and *Chaoborus alpinus* Peus feature overlapping variation and consequently he considered these forms to be conspecific. However, overlap of variation alone is not evidence of reproductive unity. Detailed analysis of character variation, distributional data and bionomic information yields superior data from which to

decide species status. This study employs all three sources of data.

However recognition of members of different species is only the initial step permitting systematists to investigate species. I therefore further undertook study of intraspecific variation of the species, including analysis of sex-associated, age-related and geographical variation, and differences between larval instars. Sources of variation of individual characters of *Chaoborus* species are not well understood. Sikorowa (1973) showed that some variation of *Chaoborus flavicans* can be considered ecotypic and Cook (1956: 32) suggested the same for *Chaoborus punctipennis* (Say) larvae. Variation in number of mandibular fan bristles, ratio of length to width of prelabral appendages, total length (Smith, 1960a: 398) and air sac length (von Frankenberg, 1915: 514) of fourth instar *Chaoborus crystallinus* (De Geer) larvae is sex-associated. Total length and color of *Chaoborus americanus* (Johannsen) fourth instar larvae is also sex-associated (Bradshaw, 1973: 1249) as well as reflecting a polymorphism. Roth (1967: 66) noted worn prelabral appendages of overwintered fourth instar larvae of *Chaoborus albatius* Johnson. Seasonal differences of total length of mature fourth instar larvae of *Chaoborus punctipennis* was reported by Muttkowski (1918: 407). *Chaoborus punctipennis* adult size (Cook, 1956: 32) and number of mandibular fan bristles of *Chaoborus anomalus* Edwards fourth instar larvae (McGowan, 1972: 365) may vary geographically. All these studies suggest possible sources of variation and I have attempted to provide interpretations of variation of characters of species of *Schadonophasma* in light of these previous studies.

Systematic studies should be based on evolutionary theory and the aforementioned analyses provide a sufficient background from which to hypothesize the evolutionary history of the subgenus *Schadonophasma* and to also propose a possible example of sympatric speciation. An interpretation of the phylogeny of some *Chaoborus* species is provided.

Because of their importance as fish food (Goldspink and Scott, 1971; Green *et al.*, 1973; Kruger, 1973; Lindquist *et al.* 1943; MacDonald, 1956; Pope *et al.*, 1973), as mosquito predators (Montchadsky, 1964; Sailer and Lienk, 1954; Skierska, 1969, 1974), in the prominent role they play in fresh water communities (e.g. Bonomi, 1962; Fedorenko and Swift, 1972; Juday, 1921; Miyadi, 1932; Miyadi and Hazema, 1932; Petr, 1972; Swüste *et al.*, 1973; Woodmansee and Grantham, 1961) and occasionally as pests (Brydon, 1956; Herms, 1937; Hitchcock, 1965; Lindquist and Deonier, 1942a, 1942b; Lindquist *et al.*, 1951; MacDonald, 1953, 1956; Shemanchuk, 1959) many *Chaoborus* populations are better known bionomically than systematically. For example, although *Chaoborus flavicans* has been studied ecologically in detail (e.g. Balvay, 1977d; Parma, 1971b), no thorough distributional study has been done on this species or any other species of the Holarctic region. This situation allows systematists working on *Chaoborus* to take into account a wide array of ecological work and to draw systematic inferences from such studies.

Chaoborus is composed of medium sized flies 2.0–9.3 mm in length. Adults of this genus are not known to bite although the most primitive genus of the family, *Corethrella* Coquillett, includes species with haematophagous adults (McKeever, 1977; Miyagi, 1974, 1975; Williams and Edman, 1968). In the Holarctic region larvae may be commonly found in permanent and temporary lentic waters and occasionally in rivers.

Chaoborus includes 37 described species in six subgenera (*Neochaoborus* Edwards, *Sayomyia* Coquillett, *Edwardsops* Lane, *Peusomyia* Saether, *Schadonophasma*, and *Chaoborus sensu stricto*). The genus has been recorded from most major land masses with the exception of New Zealand, Antarctica, Greenland, and most oceanic islands. Edwards (1932) gave a world list of species and their distribution. The Palaearctic species have been described most recently by Hirvenoja (1961), Martini (1931), Parma (1969), Peus (1934), Prokesova (1959), and Sikorowa (1967a, 1973) and Nearctic species by Dyar and Shannon (1924) and Cook (1956) who also provided a detailed morphological

study. Saether (1970) gave the most recent revision of Palaearctic and Nearctic species and was first to compare material of most species from both these regions. Palaearctic and Nearctic samples of *Chaoborus flavicans* were studied by Saether (1967). Saether (1972) presented keys to fourth instar larvae, pupae and adults of species of the Holarctic region and gave a synopsis of their way of life and structure.

Lane (1953) and Saether (1976) have provided descriptions for most known species of *Chaoborus* in South America. African species have been described by Edwards (1930), Green and Young (1976), McGowan (1972, 1976), and Verbeke (1957, 1958) and Oriental and Australian species by Giles (1902, 1904), and Theobald (1901b, 1903). Fossil species have been described by Borkent (1978b), Edwards (1923), von Heyden (1862), Meunier (1904), and Scudder (1890; questionable identification).

The objects of this study were species of the subgenus *Schadonophasma*, whose adults and larvae are the largest of *Chaoborus* species. Species are restricted to northern boreal regions. Larvae of all species sometimes occur in large numbers in permanent and temporary lentic waters. Adults and immatures are poorly represented in museum collections.

Most descriptions are brief and bionomic information anecdotal (Allan, 1973; Anderson and Raasveldt, 1974; Dickenson, 1944; Dodson, 1970; Dyar and Shannon, 1924; Edwards, 1932; Felt, 1904, 1905; Giles, 1902; Hamilton, 1971; James *et al.*, 1969; James and Smith, 1958; Jenkins and Knight, 1950; Johannsen, 1903, 1934; Loew, 1862; Matheson, 1944, 1945; Pope *et al.*, 1973; Smith, 1960b; Theobald, 1901b; Tullock, 1934; Twinn *et al.*, 1948; Zetterstedt, 1838, 1851). The feeding characteristics and vertical migration of the larvae and the life cycle of *Chaoborus trivittatus* (Loew) from Eunice Lake, British Columbia have been described by Fedorenko (1975a, 1975b, 1975c), Federenko and Swift (1972), Swift (1975, 1976), and Swift and Fedorenko (1975).

Schadonophasma was erected as a subgenus by Dyar and Shannon (1924) to contain the North American species *Chaoborus trivittatus*. Edwards (1932), Cook (1956), Matheson (1944), and Peus (1967) considered *Chaoborus nyblaei* (Zetterstedt) to be conspecific with *Chaoborus trivittatus*. Hirvenoja (1961), however, considered these to be two distinct species. Saether (1970) recognized, on morphological grounds, *Chaoborus nyblaei* in Fennoscandia and Baffin Island, Canada, and *Chaoborus trivittatus*, *Chaoborus cooki* Saether and *Chaoborus brunskilli* Saether in North America.

This study clarifies the above confusion concerning species of *Schadonophasma*.

MATERIALS AND METHODS

Materials

This study was based on examination of 293 eggs of *Chaoborus cooki*, more than 50 egg masses of *Chaoborus trivittatus*, and of all species, 49 first instar, 58 second instar, 139 third instar, and 832 fourth instar larvae, 93 male and 80 female pupae or pupal exuviae and 311 male and 248 female adults. Eggs and most adults were preserved in fluid and members of other stages and some adults were mounted on microscope slides. Many more specimens of all stages, preserved in fluid, were studied. All *Schadonophasma* material examined by Saether (1970), except the female pupa of *Chaoborus trivittatus*, was reexamined. I have also examined material collected by Osten Sacken (MCZ) but, because I could not interpret the locality labels, did not include the material in this study.

For comparative purposes (diagnostic and phylogenetic) I also examined various stages of other species of *Chaoborus*, *Mochlonyx* Loew, and *Eucorethra* Underwood. (Table 1).

Because I wanted to sample a wide geographical area and sampling lakes would have taken too much time, I collected immatures only from smaller water bodies and depended on loans for material from lakes. Place names in Alberta referred to in the text are indicated in Figure 1.

Table 1. Material other than *Schadonophasma* examined. ⊗ = undescribed material.

	First Instar	Second Instar	Third Instar	Fourth Instar	Pupae	Adults
<i>Chaoborus americanus</i>		⊗	⊗	x	x	x
<i>Chaoborus crystallinus</i>		⊗	⊗	x	x	x
<i>Chaoborus flavicans</i>	x	⊗	⊗	x	x	x
<i>Chaoborus obscuripes</i>			⊗			
<i>Chaoborus punctipennis</i>				x	x	x
<i>Chaoborus albatus</i>				x		
<i>Chaoborus pallidipes</i>		⊗	⊗	x		
<i>Chaoborus anomalus</i>		⊗	⊗	x		
<i>Chaoborus certapogones</i>		⊗	⊗	x		
<i>Chaoborus fuliginosus</i>	⊗	⊗	⊗	x		
<i>Mochlonyx velutinus</i>			⊗	x	⊗	x
<i>Eucorethra underwoodi</i>	⊗	⊗	⊗	x	x	x

Voucher specimens from this study and some of the material I collected are in the Stickland Museum, Department of Entomology, University of Alberta, Canada. Other material collected is deposited in museums as indicated in the list of localities at the end of species descriptions.

Nearly all immatures and about half of all adults were collected by myself, mostly in Alberta. The remainder were borrowed from the following museums or persons designated in the text by the following abbreviations. Names of curators are also given to facilitate inquiries about their collections.

- ABOr A. Borkent, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada, T6G 2E3.
- BMNH British Museum (Natural History), London, England, SW7 5BD; P.S. Cranston.
- CAS California Academy of Sciences, San Francisco, California, USA, 94118; P.H. Arnaud.
- CNC Biosystematics Research Institute, Research Branch, Agriculture Canada, Ottawa, Ontario, K1A 0C6; D.M. Wood.
- CUNY Department of Entomology, Cornell University, Ithaca, New York, USA, 14850; L.L. Pechuman.
- EFCo E.F. Cook, Department of Entomology, Fisheries and Wildlife, University of Minnesota, St. Paul, Minnesota, USA, 55101.
- FWI Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba, Canada, R3T 2N6; D.M. Rosenberg.
- JDAI J.D. Allan, Department of Zoology, University of Maryland, College Park, Maryland, USA, 20742.
- MCZ Museum of Comparative Zoology, Cambridge, Massachusetts, USA, 02138; J.F. Lawrence.
- OASa O.A. Saether, Museum of Zoology, University of Bergen, N-5014 Bergen, Norway.
- UASM Strickland Museum, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada, T6G 2E3; G.E. Ball.
- USNM Systematic Entomology Laboratory, United States Department of Agriculture, c/o United States National Museum, NHB 168, Washington, D.C., USA, 20560; C.F. Thompson.
- WSUP Department of Entomology, Washington State University, Pullman, Washington, USA, 99163; W.J. Turner.
- ZMHF Zoological Museum, Division of Entomology, SF-00100, Helsinki 10, Finland; B. Lindeberg.

ZMLS Zoological Institute, Department of Systematics, Helgonavägen 3, S-223 62 Lund, Sweden; H. Andersson.

Methods

Collection, preservation and dissection of material. – Egg masses of *Chaoborus trivittatus*, like those of most other *Chaoborus* species, float at the surface of the water body in which they are laid. I collected these by hand picking the floating masses from the water surface with soft-tipped tweezers and dropping them into 70% ethanol. Although egg masses can be scooped from the water surface with a dip net, they stick to the netting and attempts then made to pick them up result in their disintegration. This method should be avoided if determinations of the number of eggs per egg mass are important.

Because *Schadonophasma* larvae concentrate in the shaded portions of ponds such as that provided by *Typha*, surrounding trees, or willows, it is imperative that these areas be sampled. A common method of collecting larvae is to briskly sweep an aquatic net through a water body. Many third and fourth instar larvae are benthic during daylight hours, so stirring up the bottom is important to ensure adequate samples of these stages.

First and second instar larvae, because of their small size, are best collected with a plankton net. In this study, only ponds were sampled so that the plankton net, with a mesh size of 116 μm , was thrown from the shore and hauled in. Contents of either aquatic or plankton net were washed out in a white enamel pan with three to five centimeters of water to insure that all captured specimens were retrieved. The immatures were then picked up with soft-tipped tweezers and dropped into 70% ethanol.

Pupae were collected in the same manner as larvae except that an overly brisk motion of either plankton or aquatic net will result in specimens in which the pupal horns have been lost. Pupal exuviae were commonly found on the leeward side of ponds and were collected by hand or aquatic net.

Adults were sampled by means of an aerial net. Females of *Chaoborus trivittatus* are sedentary and although they can occasionally be collected with an aerial net, are best retrieved with an aspirator from tree trunks and herbaceous plants at the periphery of ponds.

I attempted to collect adult *Schadonophasma* with light traps but with little success. Twenty-two New Jersey light traps in and around Edmonton, Alberta from June 24 to September 4, 1974 yielded only two female *Chaoborus cooki* but did yield 1065 adults of *Chaoborus sensu stricto*. A New Jersey and CDC (Communicable Disease Centre) light trap beside a pond from which *Chaoborus cooki* adults were emerging caught none. This experience corresponds to that found for mosquitoes, in which woodland species are not attracted to lights but other species are (Bidlingmayer, 1971).

Quantitative samples of immatures for life cycle studies were obtained with the plankton net which was thrown out at least six times in the same direction from the shore and dragged at least twice across the bottom, resulting in the bottom being disturbed and thereby ensuring a representative sample. The numbers of immatures in each sample were not meant to be temporally comparable, but were interpreted to reflect only percentages of an instar present at a given time.

Material, with the exception of some pinned adults, was preserved in 70% ethanol. However, retention in alcohol for long periods of time will fade specimens. Pinned specimens are required for determination of adult coloration.

All immatures measured were prepared using the method described by Saether (1972) with the following modifications. Larvae and pupal exuviae were not cleared in KOH as this is not necessary for accurate measuring or examination and clearing has resulted in some faulty observations concerning shape of the dorsal process of larvae. One antenna and both mandibles were removed from each larva while in Canada Balsam to ensure retention of these parts, especially of younger instars whose

mouthparts are easily lost. All larvae were mounted laterally and all pupae and pupal exuviae were mounted with their ventral surfaces up. Pupal exuviae should be mounted with glass chips supporting the coverslip to prevent compression of the specimen. An alternative method is to mount the specimen in Canada Balsam, which is allowed to dry for a few hours before application of the coverslip.

Schlee (1966) indicated the advantages of fluid preserved material for the examination of chironomid adults. Mainly, dried material results in distortion of some key characters. As can be expected, this is also true of chaoborid adults. Therefore, adult material which was to be examined in detail was mounted in Canada Balsam. The two antennae, head, thorax, three left legs, wings and abdomen were disarticulated. Heads, thoraces, and abdomens were cleared in hot 8% KOH, transferred to 15% acetic acid for 15 minutes, and all parts treated consecutively for at least ten minutes each with 98% ethanol, 98% ethanol layered over cedarwood oil, cedarwood oil and Canada Balsam. *Chaoborus* adults need not be so treated to be identified. Most adult material examined was pinned.

The abdomen of each pinned male, after clearing in hot 8% KOH, was placed in one of eight arbitrarily numbered wells filled with glycerine on each of a number of 7.6 x 7.6 cm microscope slides. One gonocoxite and gonostylus with the adjoining penis valve were dissected from the rest of the abdomen and examined under both stereoscopic and compound microscopes. This ensured that no *a priori* decisions were made concerning species differences. Maximum lengths of the penis valves were estimated with the aid of a compound microscope at 200X magnification. After examination, abdomens were stored in glycerine in a genitalia vial on the pin. Examination of the genitalia from different orientations is imperative for the determination of interspecific differences of the penis valve.

Abdomens of some pinned females were treated with a weak solution (three to six crystals in three drams of distilled water) of tri-sodium orthophosphate. This treatment restores dried, more or less shrivelled parts to approximately natural size and also restores eggs, if present in the abdomen, to their natural dimensions.

Number of eggs per female was determined using reared specimens killed in 70% ethanol. Eggs were easily removed and counted while in this medium.

Rearing methods and mating experiments. – All live material was reared at 20 C and a long day (18:6, light:dark) photocycle. Field collected cladocerans, copepods and chironomid larvae and laboratory reared larvae of *Culiseta inornata* provided a continual food source for the larvae. Rearings of larvae to pupae were completed with each larva in a separate Dominion Brand 473 ml wide mouthed Mason jar filled with pond water to ensure that no larvae were lost due to cannibalism.

To determine length of pupal period, larvae were reared to adulthood in 22.7 liter aquarium filled with pond water and an abundance of food. Pupae were removed on the day they appeared and kept in separate Mason jars.

In general, rearings were completed from field collected fourth instar larvae, although earlier instars were occasionally captured for rearing. Pupae were not used for rearings as capture often resulted in at least one pupal horn being broken off and consequent reduced adult emergence (Parma 1971b: 46; pers. obs.).

Adults could not be made to mate successfully in the laboratory except when decapitated males were brought into contact with CO₂ anaesthetized females, the method used for mating experiments. Adults were reared from fourth instar larvae of *Chaoborus trivittatus* collected 2.4 km west of Edmonton, Alberta, on 13-V-1976, and 16 km west of Jasper, Alberta, on 18-V-1976, *Chaoborus cooki* collected 1.4 km west of George Lake, Alberta, on 13-V-1976. After mating, each female was placed in a three dram vial with wet paper towelling and gauze was placed over the mouth of the vial. Few adults were used in these experiments because of difficulty in synchronizing adult emergence of *Chaoborus cooki* and *Chaoborus trivittatus* in the laboratory. For the purposes of this study only eggs which embryonated were considered fertilized.

Adult feeding experiment. – This experiment had two purposes; first, to see if adult *Chaoborus trivittatus* drink water and second, to determine if water uptake affects longevity. Goff (1972) tested for imbibition of water by adults of *Chironomus riparius* by coloring sucrose water with food coloring and checking excreta for color changes. This method was used with *Chaoborus trivittatus* adults to determine if imbibition of water took place.

Adult *Chaoborus trivittatus* were collected at 1500–1600 hours on May 6, 1976, 2.4 km west of Edmonton, Alberta, with an aerial net and aspirator. They were transported to the laboratory in a screened cage placed in a styrofoam container with wet paper towels. The adults were then anaesthetized with CO₂ and sorted into treatments by 2300 hours on the day of capture. Ten males were placed in each 15 mason jars and four females in each of three jars. All were kept at 20 C with a long day (18:6, L:D) photocyce. Each jar contained a 35x10 mm plastic petri dish containing 5 ml of deionized water which was either: (1) clear and available, (2) 1% blue food coloring solution (Scott Bathgate Ltd., Winnipeg, Toronto, Vancouver) and available, or (3) screened with netting to prevent the flies from drinking. I assumed uniform humidity in all jars. Fifty males and four females were used in each treatment. The low numbers of females used was due to their scarcity in the field. Some specimens were lost during the experiments and are therefore not recorded in Figure 35.

Mortality, and the presence or absence of colored excreta, were recorded every 12 hours.

Measurements and statistics. – All measured specimens are listed at the end of species descriptions. Most measurements were made with an ocular micrometer (120 divisions) through a Wild M20 compound microscope equipped with phase contrast. Total length of larvae and the Y/X wing ratio were measured with an ocular micrometer (120 divisions) through a Wild M5 stereoscopic microscope. Measurements were taken at as high a magnification as was practical to comply as far as possible with Sokal and Rohlf (1969: 15).

Terms for structures follow those used by Cook (1956), Knight (1971a, 1971b) or Laffoon and Knight (1971). It is likely that many structures of *Chaoborus* larvae are homologous to those of culcid larvae. For example, what are termed here “antennal seta” and “antennal blades” are probably homologous to the “antennal setae” of culcid larvae (Knight and Laffoon, 1971). However, until detailed comparative studies are completed, I use traditional terms.

Measurements of larval structures were those recognized as taxonomically useful by Cook (1956), Parma (1969), Saether (1970) and Sikorowa (1973). Although numbers of bristles in both mandibular fans were counted, to reduce the consequences of possibly lost bristles, only the highest number was used for analysis. Total length was measured as length of head capsule plus distance from the anterior edge of the prothorax to the tip of the abdomen exclusive of the anal tubules. Anal fan setae which are broken off at the bases can still be counted by noting the internal portion of the setae. Some anal fan setae of some larvae were reduced as compared to the other setae and these were only counted if they were at least 0.5 times as long as the longest anal fan seta. I attempted to study the chaetotaxy of larvae but found most setae too difficult to see to obtain reliable, comparative results. I did not study the shape of anal tubules. Studies by Wichard (1975) and Wigglesworth (1938) would suggest that these would exhibit too large a degree of variation to be useful in distinguishing the morphologically similar species of *Schadonophasma*.

Measurement of pupal features follows the treatment by Saether (1970). Pupal abdominal length was measured from the anterior margin of abdominal tergite I to the posterior margin of abdominal segment VIII. I found total length to be too difficult to measure accurately from slide mounted material.

Saether (1970) recorded 74 measurements and 20 ratios from males and 67 measurements and 15 ratios from females of adult *Chaoborus cooki* (♂, n=7; ♀, n=4) and *Chaoborus trivittatus* (♂, n=7; ♀, n=5). According to the results of this study these were all correctly identified, with the possible

exception of the adult male *Chaoborus trivittatus* from Lac Phillipe, Quebec. Those measurements or ratios judged, on the basis of Saether's study, to be of possible taxonomic use were studied from slide material. Two of the most important characters, penis valve shape and Y/X wing ratio were also studied from pinned material. Terms for structures of the penis valves are shown in Figure 3B. Total length of the penis valve was measured from the base of the penis valve to the tip of the claw. The characterization of penis valves was based on a study of these structures from many orientations. Because it was impossible to standardize these, future comparisons should preferably be based on orientations in which the penis valves look similar to those illustrated in this work.

All thoracic setae, except scutellar setae, of the adults were counted on one side of the thorax. Setae on tergite IX were counted for only one side.

Searches for additional characters of all stages to separate the species of *Schadonophasma*, except eggs, previously undescribed, were generally fruitless. Features which yielded no criteria for separation of the species were:

Adults. Structure of digestive tract; setal pattern on thorax; extent of coloration; sperm shape.

Male and female pupae. Reticulation of pupal horns; length/width of respiratory horn; chaetotaxy of abdominal segments II-VIII; coloration, including that of the ribs of the anal paddle; anal paddle shape; degree of serration of outer rib of paddles; length of median rib; distance of plumose seta from base of median rib; distance of plumose seta from base of median rib/length of median rib; length, width and length/width of genital lobes.

Four instar larvae. Microsculpture of head capsule; dorsal outline of head capsule; shape of antennae; curvature of long antennal blades; length of postantennal filaments; length of labrum; width of labrum; distance of long seta from anterior base of labrum; ratio of the distance of long seta from anterior base of labrum to the length of labrum; shape of maxillae; length of seta on maxillary palpus; dorsal outline of the dorsal process.

I assumed that characters, with the exception of the length of the postantennal filaments, not useful for identification of fourth instar larvae would not be useful for younger instars.

Ratios were used to describe shapes or proportions statistically and some are complemented by illustrations. Measurements used to construct ratios or ratios themselves are abbreviated as follows:

Adults

X = length of vein Rs between R-M and fork of R_{sa} and R_s (Fig. 3C)

Y = length of vein Rs between R-M and fork of R₂ and R₃ (Fig. 3C)

Z = length of vein M between R-M and fork of M₁ and M₂ (Fig. 3C)

R₃ = length of vein R₃ (Fig. 3C)

M₁ = length of vein M₁ (Fig. 3C)

Fe = femur length

Ti = tibia length

Ta₁-Ta₅ = length of tarsomeres 1-5

$\frac{L}{R} = \frac{\text{length of first tarsomere}}{\text{length of tibia}}$

$\frac{P}{U} = \frac{\text{length of penultimate antennal article}}{\text{length of ultimate antennal article}}$

$\frac{HW}{PL} = \frac{\text{head width}}{\text{prementum length}}$

$$\frac{HV}{\text{gonostylus length} \times 10} = \frac{\text{length of male}}{\text{gonostylus length} \times 10}$$

$$\frac{HR}{\text{gonostylus length}} = \frac{\text{gonocoxite length}}{\text{gonostylus length}}$$

Male and Female Pupae

$$\frac{WS}{LS} = \frac{\text{width of seventh abdominal segment (Fig. 3A)}}{\text{length of seventh abdominal segment}}$$

Larvae

$$\frac{AS}{AL} = \frac{\text{distance of antennal seta from base of antenna (Fig. 2A)}}{\text{antennal length}}$$

$$\frac{LB}{AL} = \frac{\text{length of long antennal blade (Fig. 2A)}}{\text{antennal length}}$$

$$\frac{LB}{SB} = \frac{\text{length of long antennal blade (Fig. 2A)}}{\text{length of short antennal blade}}$$

$$\frac{PAL}{PAW} = \frac{\text{prelabral appendage length (Fig. 2A)}}{\text{prelabral appendage width}}$$

Legs are referred to by the following abbreviations.

P₁ = foreleg

P₂ = midleg

P₃ = hindleg

Statistical tests were used to compare species, larval instars and sexes, to understand geographical variation and to complement the species descriptions. Descriptive statistics of samples of eight or more individuals are ranges, means, 1.5 standard deviations (SD), and two standard errors (SE) on either side of the mean. These statistics are those graphically presented in the Hubbs diagrams. For samples of less than eight, only range and mean are given. Ranges only are given for samples of two. Total lengths of larvae are expressed only as a range, as length is growth related and for the purposes of this study, further statistics would not give additional information.

Because *Schadonophasma* fourth instar larvae could not be identified on the basis of discrete characters, I employed a compound character index to recognize fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Although this index has been used primarily to recognize hybrids and analyze zones of hybridization (Freitag, 1965, and papers cited therein; Hubbs and Peden, 1969; Rising, 1970) it is also useful to distinguish morphologically similar species. Compound character indices compile an overall measure of difference to test for morphological discontinuity (i.e. reproductive isolation). Kim *et al.* (1966) have given a step by step analysis of how characters are best used in combination to distinguish similar species and I have followed most of their suggestions. However, because I was using the index to test for lack or presence of conspecificity of samples and provide a means of identification, I did not statistically test homogeneity of samples and could not determine, beforehand, the amount of overlap of character variation between species.

Differences between male and female larvae and pupae were estimated using the unpaired t-test.

Illustrations. – Most illustrations were made with the aid of a drawing tube on a Wild M20 compound microscope from slide mounted material. They complement verbal or statistical descriptions of the species and describe the complex shape and depict the various forms of adult penis valves. Shape of the lateral outline of the dorsal process is also characterized with illustrations. Penis valves were drawn with the head in a horizontal plane.

Scanning electron photomicrographs illustrate some characters.

Distribution maps are provided. Dots represent collecting sites of all stages of a species. These localities are a composite of all material examined and therefore may not accurately reflect present distributions. Details of collecting sites and dates, and stage collected of measured specimens are available at the end of each species description.

Criteria for species recognition. – I have accepted for the purposes of this study Mayr's (1969) species definition as 'groups of actually (or potentially) interbreeding populations which are reproductively isolated from such groups'. Reproductive isolation, reflected in discontinuities in variation of characters and especially in circumstances of sympatry may be used to recognize species. However, some discontinuities can be better explained by other interpretations. Circles of races, ecophenotypic or polymorphic variation may be interpreted incorrectly as reflecting barriers to gene flow and the presence of more than one species (Brown, 1959; Mayr, 1969; Ross, 1974).

When I initiated this study I suspected that *Chaoborus trivittatus* and *Chaoborus cooki* might be conspecific. I therefore undertook a study of the structure, bionomics, behavior, and development of both species and used these data as criteria for species recognition. In addition, I carried out mating experiments with adults of *Chaoborus trivittatus* and *Chaoborus cooki*. In light of the resulting concordant evidence I was better able to interpret discontinuities of morphological variation.

Lack of bionomic data and associated adults for several samples of immatures made me uncertain of their specific status. I describe and discuss these under the heading 'populations *incertae sedis*' to better define and encourage further work on the problems posed by these samples.

Although I recognized the subspecies category as useful for the recognition of some distinctive populations, the varied uses of this category has led to numerous misunderstandings of variation within species and I therefore prefer to describe variation of populations without formally classifying them.

Taxonomic Methods. – The structure of fourth instar larvae, pupae and adults of several populations of *Schadonophasma* in Alberta indicate that these were referable to previously described *Chaoborus trivittatus* and *Chaoborus cooki*. Mating experiments and study of behavior and bionomics were used to test interpretation of morphological differences as a result of reproductive discontinuities. Study of such differences was then applied to all available material to determine if these would support indications of lack of conspecificity. A compound character index was used to test for morphological discontinuities of fourth instar larvae of *Schadonophasma* and provided a means of identification of these larvae. Identification of eggs and first, second and third instar larvae was based on either laboratory rearings or association with identified later stages.

The limited material of *Chaoborus nyblaei* available from Europe presented some problems of interpretation and, although the criterion for recognizing this as a sample of a distinct species was mostly morphological, interpretation of functional significance of some morphological features was also used.

Geographical variation was studied for two purposes. One was to test my concepts of biological species and the other, to better understand the extreme variation and evolutionary history of the species.

Paucity of material limited the stages studied for geographical variation of characters, to fourth instar larvae and adults.

For the study of geographical variation of characters the most informative statistic is the mean. To investigate patterns of variation I plotted mean values of a character for all samples which contained eight or more individuals, on a map of North America or Alberta and visually judged if any patterns were present. Samples of less than eight were lumped with the geographically closest sample.

The geographical variation of all characters of the fourth instar larvae used in the compound character index, of the penis valve length, number of setae on tergite IX of the male adults, and for Y/X wing ratio of both male and female adults, was studied in detail. Male and female adults were analyzed separately.

The correct naming of taxa was confirmed by examination of types.

I discuss my approach to the evolutionary history of species of *Schadonophasma* in the section on phylogeny and zoogeography.

Literature. – Using the very complete bibliography dealing with *Chaoborus* compiled by Roth and Parma (1970) as a basis, I attempted to trace every published account of species of *Schadonophasma* up to at least September, 1977.

Because much ecological work is dependent on correct recognition of the species studied, I have attempted to reidentify every published record either by examination of the original material or on the basis of published distributional and ecological information.

CLASSIFICATION

Genus *Chaoborus*

Edwards (1932) gave a complete list of generic synonyms (with the exception of *Edwardsops* Lane) and Cook (1956) and Saether (1972) described the general structure of *Chaoborus* species. Only additions and corrections to those descriptions are given here. The first, second and third instar larvae are fully described as they differ from fourth instar larvae. Within a species, earlier instars differ from later instars in numerous characteristics, such as head capsule length, antennal length, postantennal filament length, number of mandibular fan bristles and number of anal fan setae and these are described for *Schadonophasma* larvae in a later section. Only qualitative or non-varying differences are described here. Descriptions of earlier instars of *Chaoborus* species are given by Deonier (1943), McGowan (1972), Parma (1969, 1971a), Prokesova (1959), Saether (1967, 1970), Sikorowa (1973) and Smith (1960a). Eggs or egg masses have been described by Aitken (1954), Berg (1937), Herms (1937), Lindquist and Deonier (1942b), MacDonald (1956), McGowan (1974, 1975, 1976), Parma (1971b), Sikorowa (1973), Smith (1960a) and von Frankenberg (1937).

Saether's comments on the subgenus *Sayomyia* appear to be based on only the North American species *Chaoborus punctipennis*, *Chaoborus astictopus* Dyar and Shannon, *Chaoborus albatus*, *Chaoborus annulatus* Cook, and *Chaoborus maculipes* Stone, and do not apply to at least some tropical species. Saether's (1970) calculation of HR was incorrect and actually is the inverse of the data he presented.

Some erroneous interpretations of characters differing between larval instars are discussed under the heading 'Characters Varying between Larval Instars'.

Keys to subgenera of *Chaoborus* of the Holarctic region for adults, pupae, and fourth instar larvae have been provided by Saether (1972). More comprehensive keys must await analysis of species of the Neotropical, Oriental, and Australian regions. Some corrections to Saether's (1972) keys are presented below in the key to species.

Diagnosis. – Adults. Second tarsal article shorter than first; male tarsal claws equal; tarsal claws not toothed; females with three seminal capsules; vein R_1 terminated distal to vein Cu_1 apex.

Pupae. Respiratory horns with spiracular openings small, slit-like; paddles free, movable, each supported by one medial, two marginal ribs (Fig. 2C,D).

Larvae (all instars). Head capsule laterally compressed; antennae proximate; pair of air sacs in both thorax and abdominal segment VII; no respiratory siphon; anal segment with ventral setal fan.

Description of Chaoborus. – Adults. Females with row of comb-like setae on anterior face of third tarsus of midlegs (Fig. 4A).

Pupae. Respiratory horns spindle-shaped (Saether, 1972: 272) to globular (Verbeke, 1957: 190); terminalia almost parallel

(Fig. 5B; Blanchard, 1905: 39; Deckart, 1958: 269; Prashad, 1918: 19; Senior-White, 1927: 65; Wesenberg-Lund, 1943: 418), to perpendicular (Fig. 5A) to longitudinal axis of body.

Fourth Instar Larvae. Length 4.4–20.3 mm; predaceous; developing adult eye visible (present or absent in *Chaoborus anomalus*); apex of antenna with six terminal setae (Fig. 2A); four long, one noticeably shorter, one much shorter; pair of setae dorso-posterior of antennae dendritic; ten postantennal filaments; prelabral appendages one in front of other, setaceous or laterally flattened; mandibular fan present; maxillae as shown by Parma (1971a: 175), Cook (1956: 76); anal fan setae plumose, not paired; abdominal segment IX dorsal process flat, conical or with short article.

Third Instar Larvae. Most specimens of most species with developing adult eye visible, absent from *Chaoborus anomalus*; antenna with six terminal setae; pair of setae dorso-posterior of antennae simple; ten postantennal filaments; prelabral appendages, one anterior of other, setaceous or flattened; mandibular fan present; maxillae as shown by Parma (1971a: 175); anal fan setae plumose, not paired.

Second Instar Larvae. Some specimens of some species with developing adult eye visible; antenna with six terminal setae; eight postantennal filaments; prelabral appendages lateral to one another, setaceous; mandibular fan present; maxillae as shown by Parma (1971a: 175); anal fan setae plumose, not paired.

First Instar Larvae. Developing adult eye not visible; egg burster on dorsum of head capsule; antenna with four terminal setae; base of antenna without posterior curve (except *Chaoborus edulis* Edwards; McGowan, 1976: 300); two postantennal filaments; prelabral appendages lateral to one another, setaceous; mandibular fan absent; maxillae as shown by Parma (1971a: 175); anal fan setae simple, in pairs.

Eggs. Outline oval; some species with eggs in jelly-like matrix; white when laid, later light to dark brown; chorion transparent; at least for species of *Chaoborus sensu stricto* egg shell canoe-like in shape (Parma, 1971b: 32; pers. obs.) with dorsal longitudinal slit (see also descriptions of *Schadonophasma* species).

Subgenus *Schadonophasma*

Schadonophasma Dyar and Shannon 1924: 209. TYPE SPECIES (by monotypy) *Corethra trivittata*

Loew 1862: 186. Cook 1956: 28. Edwards 1932: 26.

Schadanophasma Saether 1970: 12 (misspelling).

Saether (1970: 14) incorrectly recognized *Chaoborus nyblaei* as type species.

Especially considering the morphological similarity of known stages of *Chaoborus* species, Lane's (1951: 336) suggestion that *Chaoborus* subgenera be raised to generic rank does not seem to be justified and, at least until the world fauna is better understood, subgeneric status should be retained.

Diagnosis. — Adult. Total length 5.2–9.3 mm; general coloration as given by Cook (1956); wings with several spots (Fig. 3C); more darkly pigmented than rest of thorax-anterior pronotum, dorsal portion of posterior pronotum (some specimens not so darkly), ventral half of preepisternum, anterior half of anterior anepisternum 2, pleural apophysis, anterior-dorsal edge of anepimeron, meron, center of anepisternum 3, scutellum, postnotum, two pairs of vittae on scutum; R_{5+6} present, Cu_{2+3} faint or absent; wing veins scaled; legs each with apex of femur, apex and base of tibia, apex of first, second and third tarsomeres and, all of fourth and fifth tarsomeres darkly pigmented; pulvilli well developed, at least half as long as claws; ommatidia free, dorsal part of eye at least as long as three ommatidia (Saether, 1970: Fig. 9); no parascutellar setae. Male. Without lobe or stout setae on inner face of gonocoxite; penis valve with apical claw. Female. Inner face of tarsomere three of midlegs and hindlegs with row of comb-like setae (Fig. 4A); segment X not covered by tergite IX in dorsal aspect, neither apically bilobed (Cook, 1956: fig 15A); seminal capsule ovoid with short, slightly curved neck (Cook, 1956: fig. 14J); antenna with 13 flagellar articles.

Pupa. Overall coloration from light to dark brown, females slightly darker than males; mature specimens more darkly pigmented along posterior and anterior margin of each abdominal segment, also bases of some setae, bases of paddles; longitudinal stripes parallel to outer margin of abdominal tergite and sternite; median rib of paddle darker than lateral ribs; in some, outer and middle ribs equally pigmented but darker than inner rib; when pharate adult developed (abdominal setae of pharate adult visible) pigmented wings and legs visible, penis valves of males with apical claw (Fig. 3B); WS/LS of both male and female 1.20–1.89; median rib with plumose seta 0.47–0.79 of its length from base and simple seta near apex; shagreening at base of paddles; outer rib of paddle with only sparse shagreening; median rib almost extended to margin of paddle and curved apically (Fig. 2C,D); respiratory horns spindle-shaped; length of respiratory horn/width of respiratory horn of male 3.30–4.71, of females 3.23–4.80; chaetotaxy as shown on Figure 6, setae present as shown by Belkin *et al.* (1970) except seta 4–II present; male genital sac length 932–1298 μm , width 189–307 μm , length/width 3.24–5.05.

Fourth Instar Larva. Total length 11.4–20.3 mm; head capsule length 1404–2620 μm ; seta on anterior face of antenna inconspicuous; AS/AL 0.75–0.93; antenna with curve at posterior base (Fig. 7D); tentorium pigmented, thick, conspicuous (Fig. 2A); dorsal process on abdominal segment IX flat (Fig. 2B, 8C, D); head capsule colorless to dark brown; more pigmented specimens with posterior margin, dorsal surface on head capsule, area around anterior tentorial pit, and line of attachment of mandible conspicuously

pigmented; lateral outline of dorsal surface of head capsule as shown by Saether (1970: fig. 11A,B,C) and Figure 2A and 7I; longest mandibular tooth elongate, with curve about 0.75 from base (Fig. 8B; Saether, 1970: fig. 11K; Felt, 1904: fig. 99); head capsule with microsculpture polygonal on posterior edge (Fig. 4B); additional features in key.

Third Instar Larva. As fourth instar larva except following: total length 7.0–13.0 mm; head capsule length 944–1440 μm ; lateral outline of dorsal surface of head capsule as in Figure 7H; microsculpture on posterior margin of head capsule not obviously polygonal; antenna with curve at posterior base (Fig. 7c); AS/AL 0.53–0.90; longest mandibular tooth elongate, with or without slight curve about 0.75 from base; additional features in key.

Second Instar Larva. As fourth instar larva except following: total length 4.7–7.3 mm; head capsule length 522–760 μm ; lateral outline of dorsal surface of head capsule as in Figure 7G; microsculpture on posterior margin of head capsule not polygonal; antenna with only slight curve at posterior base (Fig. 7B); AS/AL 0.38–0.72; longest mandibular tooth elongate, without curve; additional features in key.

First Instar Larva. As fourth instar larva except following: total length 2.0–4.5 mm; head capsule length 294–494 μm ; lateral outline of dorsal surface of head capsule as shown in Figure 7E,F; microsculpture on posterior margin of head capsule not polygonal; antenna without curve at posterior base (Fig. 7A); AS/AL 0.24–0.40; mandible as in Figure 8A; additional features in key.

Description. – Description of the subgenus is provided in the description of *Chaoborus*, the diagnosis of *Schadonophasma*, and the following keys and description of species.

Key to the species of *Schadonophasma*

Species of *Schadonophasma* are morphologically very similar and are therefore difficult to identify. No single character can or should be relied upon to identify larva, pupae or adults to species; thus, to be confident of a correct determination, all characters described should be examined. Because of this overlap of range of variation it is best to identify several individuals from a sample and opposites of the couplet should be compared.

Male adults

The shape of the penis valves is particularly important but difficult to use in identifying males. It is most important that the penis valves be examined from a number of orientations until their shape approximates those illustrated.

- 1 Penis valve head elongate, with claw mostly parallel to longitudinal axis (Fig. 10A–O); penis valve length 145–232 μm ; Y/X wing ratio 1.17–3.22; length of tarsomere five of foreleg 186–273 μm ; length of claw of foreleg 53–83 μm ; coloration of vittae generally black or very dark brown..... *Chaoborus trivittatus* (Canada, eastern and western U.S.A.)
 Penis valve shape not as above (Fig. 11A–N) or if similar (Fig. 11, O,P), specimen from Fennoscandia; penis valve length 191–232 μm ; Y/X wing ratio 1.64–3.62; length of tarsomere five of foreleg 220–284 μm ; length of claw of foreleg 65–88 μm ; coloration of vittae generally brown 2
- 2 Penis valve head bulbous, with claw mostly perpendicular to longitudinal axis (Fig. 11 A–N); Y/X wing ratio 1.64–3.62; length of claw of foreleg 65–88 μm
 *Chaoborus cooki* (Canada)
 Penis valve head elongate with claw mostly perpendicular to longitudinal axis (Fig. 11 O,P); Y/X wing ratio 1.88–2.13; length of claw of foreleg about 85 μm
 *Chaoborus nyblaei* (Fennoscandia)

Female adults

Egg number and type, when present in the abdomen and in good condition, are consistent and reliable characters for species determination.

- 1 Seminal capsules 71–102 μm in diameter; Y/X wing ratio 1.19–3.22; length of tarsomere

five of foreleg 232–290 μm ; length of claw of foreleg 64–81 μm ; prementum length 325–510 μm ; coloration of vittae generally black or very dark brown; distance from anterior tip of longest ovary to apex of abdomen 0.71–1.11 times total length of abdomen of teneral females; total number of eggs 150–329 in nulliparous individuals; eggs, if present, of parous individuals with no obviously thick exochorion (Fig. 9A).....
..... *Chaoborus trivittatus* (Canada, eastern and western U.S.A.)
Seminal capsules 65–79 μm in diameter; Y/X wing ratio 2.03–5.83; length of tarsomere five of foreleg 232–325 μm ; length of claw of foreleg 64–104 μm ; prementum length 458–574 μm ; coloration of vittae generally brown; distance from anterior tip of longest ovary to apex of abdomen 0.32–0.62 times total length of abdomen of teneral females (unknown for *Chaoborus nyblaei*); total number of eggs 58–144 in nulliparous individuals; eggs, if present, of parous individuals with obvious thick exochorion (Fig. 9B,C) *Chaoborus cooki* (Canada) *Chaoborus nyblaei* (Fennoscandia)

Male and female pupae

Male and female pupae are distinguished from one another by the shape of their genital lobes (Fig. 2C,D), (Deonier, 1943: fig. 1,2).

Saether's (1972) key to pupae should read 'abdominal segment VII' instead of 'abdominal segment VIII' and couplet 7(4) (pg. 271) should read 'Median rib of anal paddle with a minute seta at apex and a single plumose seta medially (Fig. 12 O-Q); greatest width of thoracic organ at or below the middle'.

Male pupae

- 1 Width of adominal segment VII 1074–1794 μm ; respiratory horn length 1.18–1.48 mm; non-teneral live individuals with abdomen nearly vertical (Fig. 5B)
..... *Chaoborus trivittatus* (Canada, eastern and western U.S.A.)
Width of abdominal segment VII 1605–1947 μm ; respiratory horn length 1.31–1.64 mm; non-teneral live individuals with tip of abdomen nearly horizontal (unknown for *Chaoborus nyblaei* (Fig. 5A) 2
- 2 WS/LS 1.40–1.69 *Chaoborus cooki* (Canada)
WS/LS 1.63–1.74 *Chaoborus nyblaei* (Fennoscandia)

Female pupae

- 1 Width of abominal segment VII 1239–2266 μm ; WS/LS 1.25–1.62; mature individuals (pharate adult setae evident) with abdomen full of eggs; non-teneral live individuals with abdomen nearly vertical (Fig. 5B)
..... *Chaoborus trivittatus* (Canada, eastern and western U.S.A.)
Width of abdominal segment VII 1605–2382 μm ; WS/LS 1.43–1.89; mature individuals (pharate adult setae evident) with ovaries extended to, at most, abdominal segment V (unknown for *Chaoborus nyblaei*); non-teneral live individuals with tip of abdomen nearly horizontal (unknown for *Chaoborus nyblaei*) (Fig. 5A) 2
- 2 Width of abdominal segment VII 1605–2230 μm ; WS/LS 1.43–1.87
..... *Chaoborus cooki* (Canada)
Width of abdominal segment VII 2030–2384 μm ; WS/LS 1.71–1.89
..... *Chaoborus nyblaei* (Fennoscandia)

Larvae

Roman numerals refer to larval instars. *Chaoborus nyblaei* I, II, and III are unknown.

- | | | |
|---|--|---|
| 1 | Prelabral appendages one in front of other | 5 |
| | Prelabral appendages lateral to one another | 2 |
| 2 | (1) Egg burster on dorsum of head capsule (Fig. 7E,F); antennae each with four terminal setae; two postantennal filaments; mandibular fan absent; most anal fan setae arranged in pairs | 3 |
| | No egg burster on dorsum of head capsule (Fig. G-I); antennae each with six terminal setae; eight postantennal filaments; mandibular fan present; no anal fan setae arranged in pairs | 4 |
| 3 | (2) Egg burster on dorsum of head capsule not pigmented, shaped as in Figure 7K; head capsule length 294–368 μm ; antennal length 79–115 μm ; antennal blade length 176–232 μm <i>Chaoborus trivittatus</i> I (Canada, eastern and western U.S.A.) | |
| | Egg burster on dorsum of head capsule pigmented, shaped as in Figure 7J; head capsule length 347–493 μm ; antennal length 103–132 μm ; antennal blade length 208–288 μm <i>Chaoborus cooki</i> I (Canada) | |
| 4 | (2) Head capsule length 522–650 μm ; LB/AL 1.02–1.16; 8–14 mandibular fan bristles; 16–21 anal fan setae <i>Chaoborus trivittatus</i> II (Canada, eastern and western U.S.A.) | |
| | Head capsule length 638–760 μm ; LB/AL 0.91–1.07; 7–9 mandibular fan bristles; 19–26 anal fan setae <i>Chaoborus cooki</i> II (Canada) | |
| 5 | (1) Head capsule length 944–1440 μm ; antennal length 423–673 μm ; postantennal filament length 354–578 μm | 6 |
| | Head capsule length 1404–2620 μm ; antennal length 623–1235 μm ; postantennal filament length 555–1015 μm | 7 |
| 6 | (5) AS/AL 0.58–0.90; PAL/PAW 3.36–15.00; 9–24 mandibular fan bristles; 19–28 anal fan setae | |
| | <i>Chaoborus trivittatus</i> III (Canada, eastern and western U.S.A.) | |
| | AS/AL 0.53–0.81; PAL/PAW 3.56–6.60; 8–12 mandibular fan bristles; 22–23 anal fan setae <i>Chaoborus cooki</i> III (Canada) | |
| 7 | (5) Head capsule length 1404–2384 μm ; antennal length 632–1195 μm ; LB/SB 1.47–2.92; PAL/PAW 2.63–9.88; 11–36 mandibular fan bristles; 21–33 anal fan setae | |
| | <i>Chaoborus trivittatus</i> IV (Canada, eastern and western U.S.A.) | |
| | Head capsule length 1707–2620 μm ; antennal length 789–1235 μm ; LB/SB 1.14–2.13; PAL/PAW 2.00–5.30; 8–17 mandibular fan bristles; 28–40 anal fan setae | 8 |
| 8 | (7) Postantennal filament length 631–944 μm ; prelabral appendage length 186–306 μm ; PAL/PAW less than 4.16; 28–38 anal fan setae <i>Chaoborus cooki</i> IV (Canada) | |
| | Postantennal filament length 684–1015 μm ; prelabral appendage length 300–348 μm for specimens with undamaged tip (tip not coming to flat end (Fig. 15E-H)); PAL/PAW for such specimens 3.58–5.13; 34–40 anal fan setae <i>Chaoborus nyblaei</i> IV (Fennoscandia) | |

Eggs

- | | | |
|---|--|--|
| 1 | Laid in spiral arrangement in flat jelly-like matrix; exochorion thin, without obvious sculpturing (Fig. 9A; 4C); length/width 2.85–3.16 | |
| | <i>Chaoborus trivittatus</i> (Canada, eastern and western U.S.A.) | |

Laid in more or less spherical mass (unknown for *Chaoborus nyblaei*); exochorion thick, with hexagonal sculpturing (Fig. 9B,C; 4D); length/width without exochorion 2.36–2.77 (unknown for *Chaoborus nyblaei*)
 *Chaoborus cooki* (Canada), *Chaoborus nyblaei* (Fennoscandia)

Chaoborus trivittatus (Loew)

Corethra trivittata Loew 1862: 186. Holotype adult male, labelled: 'Me', 'Loew Coll.', 'Type 4050', 'trivittata'; (MCZ). Johannsen 1903: 398. Not Dyar 1902: 201.

Sayomyia trivittata; Felt 1904: 361. Felt 1905: 497.

Sayomyia knabi Dyar 1905: 16. Holotype third instar larva, labelled: 'Sayomyia trivittata (trivittata crossed out), Springfield Mass, F. Knab', '96'. A figure of the prelabral appendage on the label is identical to that drawn by Dyar 1905: 14; (USNM).

Chaoborus trivittatus; Dyar and Shannon 1924: 212. Saether 1970: 23. Johannsen 1934: 44. Dickinson 1944: 351.

Chaoborus trivattus Saether 1970: 23 (misspelling).

Chaoborus nyblaei; Cook 1956: 28 in part (not Zetterstedt). Saether 1970: 14 in part. Matheson 1944: 94.

Chaoborus brunskilli Saether 1970: 21. NEW SYNONYMY. Details of holotype and paratype given by Saether (1970). Label of holotype reads 'L. 244' but this is probably incorrect and should read 'L. 241'; (CNC).

Characters tested to distinguish adults of *Schadonophasma* species are described here to supplement those descriptions by Saether (1970).

Descriptions. — Males. General coloration of most specimens dark grayish brown; specific pigmentation as other members of subgenus; vittae generally black or very dark brown; penis valves as shown in Fig. 10A–O. Measurements and proportions: see Table 2.

Females. Coloration as for males. Measurements and proportions: see Table 3.

Male pupae. Non-teneral live individuals with tip of abdomen nearly vertical when at rest (Fig. 5B); coloration as other members of subgenus. Measurements and proportions: see Table 4.

Female pupae. Non-teneral live individuals with tip of abdomen nearly vertical when at rest (Fig. 5B); mature individuals (pharate adult setae evident) with ovaries extended to at least abdominal segment III; coloration as other members of subgenus. Measurements and proportions: see Table 5.

Cook (1956: 31) reported respiratory horn length of specimens from Green Valley, California to be 1.02–1.13 mm.

Fourth instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 6.

Third instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 7.

Second instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 8.

First instar larvae. Egg burster on dorsum of head capsule not as prominent (Fig. 7F) as that of *Chaoborus cooki* first instar larvae; pigmentation of egg tooth and posterior margin of head capsule not nearly as dark as that of *Chaoborus cooki*; coloration of head capsule very light. Measurements and proportions: see Table 9.

Eggs. Laid in spiral arrangement in disc of jelly-like matrix; egg with thin exochorion (Fig. 9A) with very fine sculpturing (Fig. 4E) restricted to dorsal surface. Measurements and proportions: see Table 10. Egg shell as in Figure 9D.

Bionomics. — Individuals overwinter as fourth instar larvae and are mostly restricted to permanent lentic habitats ranging from small shaded ponds to large deep lakes in woodland. Although some larvae live in temporary waters, they cannot successfully overwinter in these habitats. Adults emerge under spring conditions in Alberta. Records from elsewhere indicate some multivoltine populations (p. 184).

Table 2. Descriptive statistics for male adult *Chaoborus trivittatus*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm)	18	6.4–8.6	7.62	0.90	0.28
Number postpronotal setae	24	17–45	30.9	11.2	3.0
Number supraalar setae	26	3–10	6.3	2.5	0.7
Number of supraalar setae	26	22–61	42.2	12.7	3.3
Y/X	156	1.17–3.22	1.810	0.435	0.046
Rsa vein length	21	29–232	120	87	25
P ₁ Ta ₅	20	186–273	235.2	33.4	10.0
P ₂ Ta ₅	20	191–255	228.3	26.1	7.8
P ₃ Ta ₄	17	254–383	334.0	61.6	19.9
P ₁ claw length	22	53–83	66.9	12.1	3.4
P ₁ pulvilli length	22	26–44	39.4	7.4	2.1
Gonocoxite length	20	519–732	653	99	30
Gonostylus length	24	437–637	558	85	23
HV	17	1.26–1.54	1.375	0.104	0.034
Number setae on tergite IX	110	6–21	12.5	4.8	0.6
Penis valve length	112	145–232	194.4	27.1	3.4

Table 3. Descriptive statistics for female adult *Chaoborus trivittatus*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm)	21	5.3–8.9	7.00	1.36	0.40
Length of penultimate article	18	162–191	175.9	16.3	5.1
Length of ultimate article	18	168–261	200.4	33.8	10.6
P/U	18	0.75–1.14	0.894	0.152	0.048
Head width	21	838–1132	1025	118	34
Prementum length	21	325–516	445	68	20
HW/PL	21	1.94–3.23	2.325	0.423	0.123
Length fourth palpal article	21	215–307	254	38	11
Number preepisternal setae	21	4–14	9.4	4.2	1.2
Number anepisternal setae	20	14–35	24.0	8.7	2.6
Number upper mesepimeral setae	20	10–40	20.5	11.0	3.2
Number supraalar setae	22	35–72	52.7	17.7	5.0
Y/X	110	1.19–3.22	2.118	0.563	0.072
Claw length of P ₁	18	64–87	71.5	9.9	3.1
Pulvilli length of P ₁	18	35–58	43.5	8.6	2.7
P ₁ Ta ₅	19	232–290	248.8	22.1	6.7
P ₂ Ta ₅	19	186–319	235.7	41.4	12.5
P ₃ Ti	20	2077–2844	2375	291	86
P ₃ Ta ₁	19	1204–1829	1404	251	76
P ₃ Ta ₅	19	203–297	257.6	32.3	9.8
P ₁ L/R	19	0.53–0.66	0.591	0.047	0.014
Number setae in P ₂ Ta ₃ comb	18	13–27	19.5	6.0	1.9
Number setae in P ₃ Ta ₃ comb	14	10–22	16.3	5.1	1.8
Seminal capsule diameter	16	71–103	90.6	12.0	4.0

Table 4. Descriptive statistics for male pupae of *Chaoborus trivittatus*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm)	60	4.6–6.9	5.99	0.73	0.12
Respiratory horn length (mm)	44	1.18–1.48	1.330	0.126	0.025
Respiratory horn width (mm)	43	0.27–0.44	0.352	0.066	0.014
Abdominal segment VII length	65	885–1169	1028	106	17
Abdominal segment VII width	65	1074–1794	1517	272	45
WS/LS	65	1.21–1.89	1.474	0.183	0.030

Table 5. Descriptive statistics for female pupae of *Chaoborus trivittatus*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm)	39	5.1–7.6	6.47	0.87	0.18
Respiratory horn length (mm)	24	1.20–1.77	1.467	0.246	0.067
Respiratory horn width (mm)	24	0.30–0.51	0.398	0.099	0.027
Abdominal segment VII length	37	897–1510	1158	202	44
Abdominal segment VII width	37	1239–2266	1727	381	84
WS/LS	37	1.25–1.62	1.488	0.128	0.028

Table 6. Descriptive statistics for fourth instar larvae of *Chaoborus trivittatus*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	474	1404–2384	1881	280	17
Antennal length	493	632–1195	858	144	9
LB/SB	482	1.47–2.92	2.14	0.33	0.02
LB/AL	513	0.50–0.92	0.751	0.090	0.005
AS/AL	491	0.80–0.93	0.886	0.035	0.002
Postantennal filament length	500	555–968	743	108	6
PAL/PAW	490	2.63–9.88	5.22	1.44	0.09
Number mandibular fan bristles	517	11–36	21.8	5.9	0.4
Number anal fan setae	513	21–33	28.0	2.2	0.1

Table 7. Descriptive statistics for third instar larvae of *Chaoborus trivittatus*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	80	944–1357	1127	140	21
Antennal length	83	423–650	509	91	13
LB/SB	77	1.89–2.70	2.26	0.231	0.035
LB/AL	82	0.73–0.96	0.842	0.065	0.010
AS/AL	83	0.58–0.90	0.770	0.097	0.014
Postantennal filament length	88	354–578	440	79	11
PAL/PAW	88	3.36–15.00	6.72	2.68	0.38
Number mandibular fan bristles	82	9–24	13.6	5.9	0.9
Number anal fan setae	87	19–28	23.8	3.3	0.5

Table 8. Descriptive statistics for second instar larvae of *Chaoborus trivittatus*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	18	522–650	573	44	14
Antennal length	21	215–285	241	21	6
LB/SB	20	1.81–2.38	2.08	0.235	0.070
LB/AL	21	1.02–1.15	1.09	0.058	0.017
AS/AL	20	0.53–0.72	0.605	0.078	0.023
Postantennal filament length	21	203–249	227	20	6
Number mandibular fan bristles	19	8–14	9.9	2.7	0.8
Number anal fan setae	22	16–21	18.9	1.9	0.5

Table 9. Descriptive statistics for first instar larvae of *Chaoborus trivittatus*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	26	294–368	333	31	8
Antennal length	28	79–115	97.0	11.5	2.9
LB/AL	28	1.85–2.78	2.19	0.26	0.07
AS/AL	27	0.23–0.39	0.301	0.660	0.017
Postantennal filament length	15	73.5–97.0	85.26	11.43	3.87
Number anal fan setae	26	16–23	20.0	2.4	0.6

Table 10. Descriptive statistics for eggs of *Chaoborus trivittatus*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Length	12	655–684	668	14.3	5.5
Width	12	215–232	224	8.7	3.3
Length/Width	12	2.85–3.16	2.99	0.137	0.053

Derivation of specific epithet. – The name '*trivittatus*' is derived from Latin (tri — three; vitta — stripe) and refers to the three vittae (actually four but two are very proximate) on the scutum of the adult.

Distribution. – Specimens of this species have been collected in woodland areas throughout Canada but are restricted in the United States to California, Oregon, Washington and Montana and to the northeastern States (Fig. 16,17). Lack of records from north central Canada and Alaska probably reflect lack of collecting. *Chaoborus trivittatus* is clearly restricted to woodland. Records from southern Alberta (Fig. 17), for example, are clearly the eastern limit of this species in this area. I attempted to collect east of these localities, but with no success. In the Rocky Mountains, the species has not been found above treeline. The single record from Baffin Island is suspect. No other records of *Schadonophasma* are north of treeline. However, for the sake of completeness, I have included the record on the distribution map.

Records of *Chaoborus trivittatus* from Wisconsin reported by Dickenson (1944) are undoubtedly correct. Cook's (1956) objection to the above report, in that he found one specimen to be culicine, erroneously assumed only one specimen collected. However, Dickenson (1944) also recorded larvae which could only be those of *Chaoborus trivittatus* (length of two centimeters). In addition, I have examined specimens from Vilas County, Wisconsin, which are *Chaoborus trivittatus*.

Even though I have not examined specimens of *Chaoborus trivittatus* from Churchill, Manitoba, the reports by James and Smith (1958) of overwintering larvae (see p. 184), and Twinn *et al.* (1948) of swarming adults (see p. 189) would suggest this species to be present at that locality.

Cleugh and Hauser (1971) give the exact localities for the numbered lakes near Kenora, Ontario, given below.

LOCALITIES

Male Adults

CANADA

ALBERTA: Banff, 24-VII-1918 (1 BMNH, 4 USNM); 10 mi. (16 km) W. Jasper, 4-VI-1976 (5 CNC, 5 USNM, 8 UASM, 20 ABOr); Bigoray River, oxbow lake, 25-V-1971 (1 OASa); 1.5 mi. (2.4 km) W. Edmonton, 3-V-1976 (5 CNC, 5 USNM, 25 ABOr, 7 UASM); Edmonton, 17-V-1974 (1 ABOr); BRITISH COLUMBIA: Kaslo, 13-21-VI-? (7 USNM); Terrace, 18-VI-1960 (5 CNC, 1 ABOr); Prince Rupert, 13-V-1919 (1 CNC); Atlin, 5-VII-1955 (6 CNC, 1 ABOr); Lower Post, 20-VI-1948 (2, CNC) NORTHWEST TERRITORIES: Aklavik, 28-VIII-1932 (1 USNM); Lake Harbour, Baffin Island, 7-VIII-1935 (1 CNC); NOVA SCOTIA: 4-III-1935 (reared) (1 CNC); ONTARIO: North Burgess Twp., 15-20-V-1970, (6 CNC); Black Lk., 44°46'N 76°18'W, 26-IV-1973 (8 CNC, 1 ABOr); Kenora, Lk 241, 13-VI-1968 (reared) (1 CNC); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 20-IV-1973 (3 CNC), 5-14-V-1973 (12 CNC, 2 ABOr); YUKON TERRITORY: Whitehorse, 14-21-V-1949 (5 CNC, 1 ABOr).

UNITED STATES

CALIFORNIA: Alameda Co.: Oakland, 4-V-1937 (2 CAS); Humboldt Co.: Mad River Beach, 13-VIII-1948 (7 USNM); Monterey Co.: Pacific Grove, 18-VII-1940 (2 USNM); San Luis Obispo Co.: Oceano Beach 20-VIII-1948 (1 USNM); Santa Clara Co.: Stanford University, 7-III-1903 (1 CUNY, 2 USNM), 28-V-1903 (1 USNM); MAINE: (1 MCZ); MASSACHUSETTS: Worcester Co.: Worcester, 23-IV-? (2 MCZ); Audorra (specific locality unknown), (1 USNM); NEW HAMPSHIRE: Belknap Co.: Center Harbor, (7 USNM); Rockingham Co.: Hampton, 21-IV-1906 (1 MCZ); NEW YORK: Essex Co.: Elizabethtown 10-13-VI-1904 (1 CUNY, 1 USNM); OREGON: Multnomah, Clackamas and Washington Co.: Portland, (1 USNM); WASHINGTON: Kitsap Co.: Bremerton, 2-V-1924 (1 USNM); Port Madison, 3-II-1934 (reared) (2 USNM); Hoodsport, 3-9-V-1924 (2 BMNH, 6 USNM).

Female Adults

CANADA

ALBERTA: 10 mi. (16 km) W. Jasper, 4-VI-1975 (8 ABOr, 3 CNC); 1.5 mi. (2.4 km) W. Edmonton, 13-V-1975 (15 ABOr, 8 CNC, 10 UASM); BRITISH COLUMBIA: Kaslo, 13-20-VI-? (7 USNM); Victoria, 4-X-1922 (1 CNC); Canim Lk., 23-VI-1938 (2 CNC); Terrace, 7-18-VI-1960 (8 CNC, 1 ABOr); Atlin, 5-VII-1955 (5 CNC); Lower Post, 20-VI-1948 (1 CNC); NORTHWEST

TERRITORIES: Aklavik, 28-VIII-1932 (1 USNM); ONTARIO: Cordova Mines, 7-IX-1962 (2 CNC); North Burgess Twp., 15-20-V-1970 (1 CNC); Black Lk., 44°46'N 76°18'W, 26-IV-1973 (4 CNC); QUEBEC: Old Chelsea, 20-IX-1961 (12 CNC, 1 ABOr); YUKON TERRITORY: Whitehorse, 15-V-1944 (1 CNC), 16-V-1949 (1 CNC), 15-19-V-1950 (1 CNC).

UNITED STATES

CALIFORNIA: Alameda Co.: Berkeley, 5-VI-1948 (1 USNM); Oakland, 4-V-1937 (1 CAS); Humboldt Co.: Mad River Beach, 13-VIII-1948 (7 USNM); Kings Co.: Hanford, 8-VII-1947 (1 USNM); Madero Co.: Matadero Creek, 24-V-1937 (1 CAS); Mariposa Co.: Yosemite, 15-V-1916 (1 USNM); Mendocino Co.: Garcia River, 30-VII-1948 (1 USNM); Placer Co.: NW of Cisco, Nevada Co., 16-V-1948 (1 USNM) Placer and El Dorado Co.: Lake Tahoe, 17-IX-1915 (1 USNM); San Luis Obispo Co.: Oceano Beach, 20-VIII-1948 (2 USNM); Santa Clara Co.: Stanford University, III-1903 (1 CUNY, 6 USNM); MONTANA: Glacier Co.: North Fork Rangers Station, Glacier National Park, 13-V-1926 (1 USNM), 5-VI-1926 (1 USNM); NEW HAMPSHIRE: Belknap Co.: Center Harbor, (2 USNM); Rockingham Co.: Hampton, 19-VI-1906 (1 MCZ); NEW YORK: Essex Co.: Elizabethtown, 10-11-VI-1904 (2 USNM), 25-VIII-1904 (1 CUNY); Rockland Co.: Bear Mnt., 25-IX-1927 (1 USNM); OREGON: Multnomah, Clackamas and Washington Co.: Portland, 4-VII-1934 (2 USNM); WASHINGTON: Kitsap Co.: Manitou Beach, 13-III-1934 (reared) (1 USNM); Port Madison, 3-II-1934 (1 USNM); Mason Co.: Hoodsport, 5-9-V-1924 (4 USNM).

Male Pupae

CANADA

ALBERTA: 1.5 mi. (2.4 Km.) W. Edmonton, 8-V-1974 (2 ABOr, 1 UASM); BRITISH COLUMBIA: Kaslo (4 USNM); Eunice Lk., 24-V-1971 (3 OASa); Lower Post, 19-20-VI-1948 (20 CNC); NEWFOUNDLAND: 3 mi. (4.8 km) N. St. John's, 4-VI-1975 (1 ABOr); ONTARIO: Kenora, Lk. 241, 13-VI-1968 (1 CNC); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 20-21-IV-1973 (12 CNC, 2 ABOr).

UNITED STATES

CALIFORNIA: Contra Costa Co.: Jewel Lk., 11-V-1948 (5 USNM); Humboldt Co.: Mad River Beach, 13-VIII-1948 (9 USNM); MICHIGAN: Gogebic Co.: Hummingbird Lk., 15-VIII-1971 (1 OASa); WASHINGTON: Snohomish Co.: Everett, 7-IV-1949 (3 WSUP); Hall Lk., 29-VIII-1952 (11 WSUP).

Female Pupae

CANADA

ALBERTA: 53 mi. (85 km) N. Coleman, 3-VIII-1975 (2 ABOr, 2 UASM); 1.5 mi. (2.4 km) W. Edmonton, 8-V-1974 (4 UASM); BRITISH COLUMBIA: Kaslo (4 USNM); Lower Post, 19-20-VI-1948 (8 CNC); NEWFOUNDLAND: 3 mi. (4.8 km) N. St. John's, 4-VI-1975 (1 ABOr); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 20-IV-1973 (1 CNC), 5-6-V-1973 (3 CNC).

UNITED STATES

CALIFORNIA: Contra Costa Co.: Jewel Lk., 11-V-1948 (2 USNM); Humboldt Co.: Mad River Beach, 13-VIII-1948 (8 USNM); Snohomish Co.: Hall Lk., 29-VIII-1952 (4 WSUP).

Fourth Instar Larvae

CANADA

ALBERTA: 2.5 mi. (4.0 km) NW Edmonton, 13-IX-1970 (4 ABOr); 1.5 mi. (2.4 km) W. Edmonton, 26-IV-1975 (25 ABOr, 13 CNC, 5 UASM); 2 mi. (3.2 km) N. Devon, 23-IX-1972 (1 ABOr); 4.7 mi. (7.6 km) NW Mountain Park, 21-IX-1974 (20 ABOr, 7 CNC, 5 UASM); East Henry Pond, Jasper National Park, 12-IX-1968 (1 FWI, 4 CNC); 1.5 mi. (2.4 km) S. Robb, 23-VII-1975 (50 ABOr, 6 UASM); 53 mi. (85 km) N. Coleman, 3-VIII-1975 (10 ABOr, 2 UASM); 43 mi. (69 km) N. Coleman, 3-VIII-1975 (1 ABOr); 33 mi. (53 km) N. Swan Hills, 1-IX-1975 (12 ABOr); 62 mi. (100 km) N. Coleman, 3-VIII-1975 (15 ABOr, 7 UASM); 38 mi. (61 km) N. Swan Hills, 1-IX-1975 (11 ABOr); 14 mi. (22 km) E. Fox Creek, 30-VIII-1975 (11 UASM); 1 mi. (1.6 km) N. Swan Hills, 1-IX-1975 (11 ABOr); 23 mi. (37 km) E. Fox Creek, 30-VIII-1975 (11 ABOr); 43 mi. (69 km) E. High Prairie, 1-IX-1975 (11 ABOr); 3 mi. (4.8 km) S. Hinton, 23-VII-1975 (11 ABOr); 32.5 mi. (52 km) N. Banff, 8-XI-1976 (11 ABOr); Pond nr. Kinky Lk., 11-IX-1976 (10 ABOr); 26 mi. (42 km) N. Sundre, 11-X-1976 (11 ABOr); 47 mi. (76 km) N. Nordegg, 7-IX-1976 (11 ABOr); 12 mi. (19 km) S. Seebe, 3-VIII-1975 (11 ABOr); 10 mi. (16 m) W. Jaspeer, 27-IV-1976 (10 ABOr); 58 mi. (93 km) S. Seebe, 3-VIII-1975 (11 ABOr); 28 mi. (45 km) E. Jasper, 27-IV-1976 (11 UASM); 4 mi. (6.4 km) W. Jasper, 20-V-1975 (9 ABOr); 5 mi. (8.0 km) S. Jasper, 18-VI-1975 (12 ABOr); *Pond nr. Cameron Lk., 18-IX-1977 (17 ABOr); *Pond nr. Wabamun Lk., 15-X-1977 (1 ABOr); *Opal, 10-X-1977 (6 ABOr); BRITISH COLUMBIA: 3 mi. (4.8 km) E. Sicamous, 10-VI-1976 (11 ABOr); Prince Rupert, 13-V-1919 (15 USNM); Kaslo, (5 USNM); 4.8 mi. (7.7 km) N. Clearwater, 12-VI-1976 (11 ABOr); Eunice Lk., fall of 1971 (4 OASa, 10 ABOr); Lower Post, 19-VI-1948 (11 CNC); Gwendoline Lk., ?-VIII-1973 (10 ABOr); NEWFOUNDLAND: 3 mi. (4.8 km) N. St. John's, 4-VI-1975 (11 ABOr); 0.4 mi. (0.6 km) W. Logy

Bay, 8-VII-1967 (5 USNM); ONTARIO: Kenora, Lk. 241, 14-V-1969 (3 FWI, 8 CNC); Kenora, Lk. 81, 7-V-1969 (1 FWI, 1 CNC); Kenora, Lk. 230, 14-V-1969 (2 FWI, 2 CNC); Kenora, Lk., 240, 14-V-1969 (1 FWI); *10 mi (16 km) E. Thessalon, 19-IX-1978 (18 ABO); *Kendel, 15-V-1973 (3 ABO), 17-VII-1973 (2 ABO); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 21-IV-1973 (17 CNC); Lk. a la Croix, 26-VI-1971 (2 OASa, 10 ABO); Randin Lk., 19-VI-1974 (10 ABO); YUKON TERRITORY: Klutlan Glacier moraine, VII-1971 (6 EFCo, 3 ABO).

UNITED STATES

CALIFORNIA: Contra Costa Co.: Jewel Lk., II-V-1948 (4 USNM); Humboldt Co.: Mad River Beach, 13-VIII-1948 (12 USNM); Santa Clara Co.: Stanford University, ?-II-1945 (3 EFCo, 11 USNM); MAINE: Piscataquis Co.: Milo, 6-I-1906 (1 USNM); MASSACHUSETTS: Hampden Co.: Springfield, ?-VII-1903 (1 USNM); MONTANA: Meagher Co.: *27 mi. (43 km) N. White Sulphur Springs, 27-X-1978; MICHIGAN: Gogebic Co.: Hummingbird Lk., 15-VIII-1971 (3 OASa, 8 JDAI); Ziesnis Bog, 24-VIII-1971 (1 OASa); WASHINGTON: Pacific Co.: 10 mi. (16 km) S. South Bend, 19-VI-1977 (1 ABO); Snohomis Co.: Hall Lk., 8-V-1953 (10 WSUP); WISCONSIN: Vilas Co.: Forest Service Bog, 24-VIII-1971 (1 OASa).

Third Instar Larvae

CANADA

ALBERTA: 62 mi. (100 km) N. Coleman, 3-VIII-1975 (7 ABO, 2 UASM); 53 mi. (85 km) N. Coleman, 3-VIII-1975 (1 ABO); 1.5 mi. (2.4 km) S. Robb, 23-VII-1975 (25 ABO, 5 CNC); 4.7 mi. (7.6 km) NW Mountain Park, 21-IX-1974 (2 ABO); BRITISH COLUMBIA: 4.8 mi. (7.7 km) N. Clearwater, 12-VI-1976 (7 ABO); ONTARIO: Kenora, Lk. 230, 14-V-1969 (2 FWI); Kenora, Lk. 241, 13-VI-1968 (1 FWI, 8 CNC); YUKON TERRITORY: Klutlan Glacier moraine, VII-1971 (22 EFCo).

UNITED STATES

MASSACHUSETTS: Hampden Co.: Springfield, (1 USNM), ?-VIII-1903 (5 USNM).

Second Instar Larvae

ALBERTA: 62 mi (100 km) N. Coleman, 3-VIII-1975 (6 ABO, 2 CNC, 2 UASM); East Henry Pond, Jasper National Park, 12-IX-1968 (4 FWI); NEWFOUNDLAND: 3 mi. (4.8 km) N. St. John's, 4-VI-1975 (1 ABO); ONTARIO: Kenora, Lk. 230, 14-V-1969 (5 FWI); Kenora, Lk. 240, 14-V-1969 (1 FWI); QUEBEC: Randin Lk., 19-VI-1974 (2 ABO).

First Instar Larvae

ALBERTA: 1.5 mi. (2.4 km) W. Edmonton, 26-VI-1975 (10 ABO, 4 CNC); 10 mi. (16 km) W. Jasper, 18-VI-1975 (8 ABO, 4 UASM); 20 mi. (32 km) W. Edson 9-IX-1976 (1 ABO); East Henry Pond, Jasper National Park, 12-IX-1968 (1 CNC); NEWFOUNDLAND: 3 mi. (4.8 km) N. St. John's, 4-VI-1975 (1 ABO).

Eggs

ALBERTA: 10 mi. (16 km) W. Jasper, 31-V-1976 (12 egg masses ABO, 2 egg masses CNC, 2 egg masses UASM).

*Material identified but not measured.

Taxonomic notes. – Historically, recognition of specimens of this taxon has presented difficulties. Edwards (1932: 26) incorrectly synonymized *Chaoborus trivittatus* with *Chaoborus nyblaei*. *Chaoborus trivittatus* and *Chaoborus punctipennis* were erroneously considered conspecific by Brunetti (1911: 229), Dyar (1902: 201), Giles (1902: 502) and Theobald (1901b: 296; 1905: 43). Distributional information and/or type of habitat in which larvae were found suggest that Allan (1973; original material examined), Dodson (1970), Main (1953; original material examined), Maleug and Hasler (1967), Myklebust (1966), Stahl (1966) and Teraguchi and Northcote (1966) incorrectly identified specimens of *Chaoborus trivittatus* as *Chaoborus nyblaei*. Some specimens examined by Smith (1960b) were probably larvae of *Chaoborus trivittatus* as indicated by the number of anal fan setae and PAL/PAW. Similarly, data about overwintering larvae studied by James and Smith (1958) at Churchill, Manitoba indicate that these were individuals of *Chaoborus trivittatus*. I was unable to confirm the identification of some specimens from British Columbia collected by Hearle (1928) as *Chaoborus trivittatus*.

Shape of the penis valve of the type specimen (Fig. 10 O) confirmed the naming of this species.

Examination of the type of *Sayomyia knabi* showed that the diagnostically (for that geographical

region) thick tentorium of the larvae of *Chaoborus trivittatus* was present. All measurements were within the range of the third instar larvae of *Chaoborus trivittatus*. In addition, the pharate fourth instar larva was evident.

All diagnostic features of *Chaoborus brunskilli* (Saether, 1970: 21) are within range of variation of *Chaoborus trivittatus*. Penis valves of the holotype, when reoriented (Fig. 10M), were inseparable from those of *Chaoborus trivittatus*. Specimens of *Chaoborus brunskilli* mentioned by Anderson and Raasveldt (1974) and Hamilton (1971) are therefore *Chaoborus trivittatus*.

The identification of the specimen from Lac Phillipe, Quebec, as *Chaoborus trivittatus* by Saether (1970) could not be confirmed as the penis valves were distorted. I have not included the specimen in this description.

Previous descriptions of pupae are given by Saether (1970) (as *Chaoborus trivittatus* and *Chaoborus brunskilli*), by Cook (1956) (as *Chaoborus nyblaei*) and by Felt (1904).

The only useful previous descriptions of fourth instar larvae are those by Saether (1970) (as *Chaoborus trivittatus* and *Chaoborus brunskilli*) and Felt (1904). Cook's (1956) description of larvae of *Chaoborus nyblaei* undoubtedly included specimens of both *Chaoborus trivittatus* and *Chaoborus cooki* (see especially description of head capsule length and PAL/PAW).

Saether (1970) gave the only previous descriptions of first, second and third instar larvae of *Chaoborus trivittatus* (as *Chaoborus brunskilli*).

Chaoborus cooki Saether

Chaoborus cooki Saether 1970:18. Details of holotype, allotype and paratypes given by Saether (1970); (CNC).

Chaoborus nyblaei; Cook 1956: 28, in part (not Zetterstedt).

Characters tested to distinguish between adults of *Schadonophasma* species are described here to supplement the descriptions by Saether (1970).

Description. — Males. General coloration of most specimens light grayish brown; specific pigmentation as other members of subgenus; vittae generally brown; penis valves as shown in Fig. 11A-N. Measurements and proportions: see Table 11.

Females. Coloration as for males. Measurements and proportions: see Table 12.

Male pupae. Non-teneral individuals with tip of abdomen nearly horizontal when at rest (Fig. 5A); coloration as other members of subgenus. Measurements and proportions: see Table 13.

Female pupae. Non-teneral individuals with tip of abdomen nearly horizontal when at rest (Fig. 5A); mature individuals (pharate adult setae evident) with ovaries extended at most to abdominal segment V. Measurements and proportions: see Table 14.

Fourth instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 15.

Third instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 16.

Second instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 17.

First instar larvae. Egg burster on dorsum of head capsule prominent (Fig. 7E), pigmented; posterior margin of head capsule noticeably pigmented. Measurements and proportions: see Table 18.

Eggs. Laid in spherical mass with slight amount of jelly-like matrix; egg with thick exochorion (Fig. 9c), with polygonal sculpturing (Fig. 4D). Measurements and proportions: see Table 19. Egg shell as in Fig. 9E.

Bionomics. — Overwinters as egg, immatures restricted to temporary occasionally permanent ponds in woodland. Larvae may be collected only during summer months (Fig. 25B). Adults generally emerge later in season than do those of *Chaoborus trivittatus*.

Derivation of specific epithet. — Named after Dr. E.F. Cook.

Distribution. — Specimens of *Chaoborus cooki* have been collected only from Canada and Alaska (Fig. 18,19). Collecting in Alberta has shown that the species is restricted to woodland. Paucity of records, as compared to *Chaoborus trivittatus* is explained by lack of collecting in the restricted habitat in which the species is found, and the presence of larvae only during the summer months.

Table 11. Descriptive statistics for male adult *Chaoborus cooki*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm)	14	6.8–9.3	7.81	1.39	0.50
Number pronotal setae	15	19–51	29.2	13.4	4.6
Number postpronotal setae	15	3–17	6.6	6.2	2.1
Number supraalar setae	15	32–48	40.4	9.1	3.1
Y/X	89	1.64–3.62	2.47	0.578	0.082
Rsa vein length	15	162–377	256	97	33
P ₁ Ta ₅	12	220–284	260.5	31.9	12.3
P ₂ Ta ₅	14	220–284	256.8	31.9	11.4
P ₃ Ta ₄	13	278–435	375.0	69.3	25.6
P ₁ claw length	15	65–88	73.6	10.6	3.6
P ₁ pulvilli length	15	41–65	49.0	9.8	3.4
Gonocoxite length	15	649–838	755	102	35
Gonostylus length	15	507–732	616	87	20
HV	14	1.05–1.53	1.293	0.260	0.093
Number setae on tergite IX	59	7–17	11.0	3.1	0.5
Penis valve length	49	191–232	211.8	16.7	3.2

Table 12. Descriptive statistics for female adult *Chaoborus cooki*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm)	17	5.3–8.5	6.54	1.38	0.45
Length of penultimate article	18	168–226	194.3	21.2	6.6
Length of ultimate article	18	168–237	206.5	33.2	10.4
P/U	18	0.83–1.21	0.953	0.147	0.046
Head width	19	944–1274	1061	120	37
Prementum length	19	441–580	504	56	17
HW/PL	19	1.85–2.44	2.110	0.195	0.060
Length of fourth palpal article	19	191–302	262	38	1
Number anepisternal setae	19	5–13	8.1	3.4	1.0
Number upper mesepimeral	19	8–30	18.6	7.0	2.1
Number upper mespimeral setae	18	9–28	16.6	6.8	2.2
Number supraalar setae	19	38–92	52.4	20.3	6.2
Y/X	100	2.03–5.83	3.741	1.098	0.146
Claw length of P ₁	17	64–104	75.4	17.7	5.7
Pulvilli length of P ₁	17	35–58	42.3	10.5	3.4
P ₁ Ta ₅	17	232–325	271.9	43.4	14.1
P ₂ Ta ₅	15	220–319	262.5	47.4	16.2
P ₃ Ti	17	2289–3092	2652	299	97
P ₃ Ta ₁	17	1204–1829	1599	248	80
P ₃ Ta ₅	15	249–348	282.3	39.3	13.5
P ₁ L/R	16	0.52–0.68	0.599	0.056	0.019
Number setae in P ₂ Ta ₃ comb	15	8–16	12.0	4.0	1.4
Number setae in P ₃ Ta ₃ comb	14	5–14	7.7	3.7	1.3
Seminal capsule diameter	18	65–79	69.8	5.9	1.8

Table 13. Descriptive statistics for male pupae of *Chaoborus cooki*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm)	11	5.6–7.7	6.67	1.01	0.41
Respiratory horn length (mm)	11	1.32–1.64	1.546	0.144	0.058
Respiratory horn width (mm)	11	0.32–0.45	0.39	0.05	0.02
Abdominal segment VII length	11	968–1227	1145	124	50
Abdominal segment VII width	11	1605–1947	1809	180	72
WS/LS	11	1.40–1.69	1.584	0.148	0.059

Table 14. Descriptive statistics for female pupae of *Chaoborus cooki*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm)	28	5.3–7.6	6.37	1.05	0.26
Respiratory horn length (mm)	25	1.37–1.82	1.631	0.149	0.040
Respiratory horn width (mm)	25	0.34–0.51	0.439	0.072	0.019
Abdominal segment VII length	28	1074–1357	1220	111	28
Abdominal segment VII width	28	1605–2230	2027	223	56
WS/LS	28	1.43–1.87	1.664	0.182	0.046

Table 15. Descriptive statistics for fourth instar larvae of *Chaoborus cooki*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	210	1707–2620	2150	255	23
Antennal length	210	789–1235	1001	122	11
LB/SB	201	1.14–2.13	1.52	0.22	0.02
LB/AL	201	0.41–0.81	0.628	0.146	0.014
AS/AL	210	0.79–0.93	0.854	0.036	0.003
Postantennal filament length	210	631–944	802	74	7
PAL/PAW	210	2.11–5.18	3.32	0.84	0.08
Number mandibular fan bristles	213	10–17	13.4	1.8	0.2
Number anal fan setae	211	28–38	32.7	2.4	0.2

Table 16. Descriptive statistics for third instar larvae of *Chaoborus cooki*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	49	1015–1440	1288	158	30
Antennal length	50	464–673	573	75	14
LB/SB	46	1.67–2.30	1.99	0.240	0.047
LB/AL	49	0.64–0.96	0.794	0.146	0.028
AS/AL	50	0.53– 0.81	0.692	0.101	0.019
Postantennal filament length	50	413–543	471	43	8
PAL/PAW	46	3.55–6.60	5.14	1.21	0.24
Number mandibular fan bristles	50	8–12	10.3	1.2	0.2
Number anal fan setae	50	22–33	28.6	3.3	0.6

Table 17. Descriptive statistics for second instar larvae of *Chaoborus cooki*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	35	638–760	712	51	11
Antennal length	33	273–347	309	23	5
LB/SB	28	2.02–2.97	2.49	0.328	0.083
LB/AL	34	0.91–1.07	0.99	0.058	0.013
AS/AL	33	0.42–0.56	0.479	0.053	0.012
Postantennal filament length	34	215–267	241	19	4
Number mandibular fan bristles	34	7–9	7.9	0.8	0.2
Number anal fan setae	35	19–26	22.0	2.4	0.5

Table 18. Descriptive statistics for first instar larvae of *Chaoborus cooki*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	20	347–494	432	69	20
Antennal length	20	103–132	117.0	13.5	4.0
LB/AL	20	1.88–2.45	2.15	0.23	0.07
AS/AL	20	0.27–0.38	0.333	0.051	0.015
Postantennal filament length	20	79.4–123.5	93.93	15.24	4.54
Number anal fan setae	19	20–26	23.0	2.4	0.7

Table 19. Descriptive statistics for eggs of *Chaoborus cooki*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Length with exochorion	13	731–853	804	43.2	17.8
Width with exochorion	13	418–458	431	16.1	6.0
Length/width	13	1.70–2.01	1.86	0.126	0.046
Length without exochorion	13	516–563	530	18.0	6.6
Width without exochorion	13	203–220	214	7.5	2.8
Length/width	13	2.37–2.77	2.47	0.153	0.056

LOCALITIES

Male Adults

ALBERTA: nr. George Lk., 30-VII-1974 (1 ABO_r); 0.9 mi. (1.4 km) W. George Lk., 13-V-1976 (reared) (20 ABO_r, 15 CNC, 10 UASM); Edmonton, 1-VII-1974 (1 ABO_r); MANITOBA: Gillam, 19-VI-1950 (1 OASa), 29-30-VI-1950 (6 CNC); Churchill, 24-VII-1947 (1 CNC), 19-VII-1951 (1 CNC), VII-VIII-1950 (4 CNC); NORTHWEST TERRITORIES: Yellowknife, 6-VII-1949 (2 CNC), 17-VII-1949 (1 CNC); Reindeer Depot, 13-VII-1949 (2 CNC); ONTARIO: Chisholm, 5-VI-1959 (4 CNC), 19-VI-1959 (1 CNC); QUEBEC: Great Whale River, 28-31-VII-1949 (6 CNC); 13-29-VIII-1949 (2 CNC, 1 OASa); YUKON TERRITORY: Whitehorse, 11-24-VII-1950 (7 CNC); Mi. 87 (Km 140), Dempster Hwy., 27-30-VI-1973 (8 CNC), 8-13-VII-1973 (11 CNC), 16-17-VII-1973 (6 CNC), 4-8-VIII-1973 (4 CNC).

Female Adults

ALBERTA: 0.9 mi. (1.4 km) W. George Lk., 13-V-1976 (reared) (10 ABO_r, 5 CNC, 3 UASM); MANITOBA: Churchill, 22-30-VII-1948 (14 CNC), VII-VIII-1950 (10 CNC), 17-VIII-1951 (1 CNC); ONTARIO: Chisholm, 19-VI-1957 (6 CNC), 3-VI-1959 (1 CNC); QUEBEC: Great Whale River, 29-VIII-1949 (1 CNC); Indian House Lake, 17-VII-1954 (1 CNC); YUKON TERRITORY: Whitehorse, 3-VII-1919 (1 CNC), 7-22-VII-1950 (5 CNC), 1-VIII-1950 (1 CNC); Mi. 87 (Km 140), Dempster Hwy. 8-13-VII-1973 (15 CNC), 16-17-VII-1973 (17 CNC); 4-8-VIII-1973 (17 CNC).

Male Pupae

ALBERTA: 33 mi. (53 km) S. Jasper, 4-VI-1975 (3 ABO_r, 3 UASM); 1.5 mi. (2.4 km) S. Robb, 23-VII-1975 (3 ABO_r); NORTHWEST TERRITORIES: Yellowknife, 6-VII-1949 (3 OASa), 14-VII-1949 (1 CNC); YUKON TERRITORY: Mi. 87 (Km 140), Dempster Hwy., 13-VII-1973. (1 CNC).

Female Pupae

ALBERTA: 43 mi. (69 km) N. Coleman, 3-VIII-1975 (5 ABO_r, 5 UASM); 20 mi. (32 km) W. Edson, 17-VI-1975 (4 ABO_r, 2 CNC, 2 UASM); BRITISH COLUMBIA: 4.8 mi. (7.7 km) N. Clearwater, 12-VI-1976 (4 ABO_r); YUKON TERRITORY: Mi. 87 (Km 140), Dempster Hwy., 13-VII-1973 (8 CNC).

Fourth Instar Larvae

ALBERTA: 43 mi. (69 km) N. Coleman, 3-VIII-1975 (13 ABO_r); 33 mi. (53 km) S. Jasper, 4-VI-1975, (5 ABO_r, 6 UASM); 1 mi. (1.6 km) S. Jasper, 4-VI-1975 (30 ABO_r, 15 UASM, 17 CNC); 14.5 mi. (23.3 km) W. Jasper 21-VI-1975 (8 ABO_r); 4 mi. (6.4 km) W. Jasper, 20-V-1975 (9 ABO_r); 20 mi. (32 km) W. Edson, 5-VI-1975 (15 ABO_r, 5 CNC, 4 UASM); 29-V-1976 (3 ABO_r); 1.5 mi. (2.4 km) S. Robb, 23-VII-1975 (2 ABO_r); 1.5 mi. (2.4 km) W. Edmonton, 12-VI-1975 (5 ABO_r, 3 UASM); 0.9 mi. (1.4 km) W. George Lk., 12-V-1975 (5 ABO_r, 5 CNC, 3 UASM); BRITISH COLUMBIA: 4.8 mi. (7.7 km) N. Clearwater, 12-VI-1976 (1 ABO_r); MANITOBA: Gillam, 10-VI-1950 (1 CNC); Churchill, 1-11-VII-1943 (1 USNM), 29-VI-1950 (1 CNC) *nr. Childs Lk., 27-V-1978 (39 ABO_r); NORTHWEST TERRITORIES: Pond nr. Harris River, 2-VI-1973 (1 CNC); ONTARIO: Aberfoyle, 14-V-1974 (1 ABO_r); YUKON TERRITORY: Dempster Hwy., 23-30-VI-1972 (13 ABO_r); Mi. 87 (Km 140), Dempster Hwy., 13-VII-1973 (11 CNC); Klutlan Glacier moraine, VII-1971 (20 EFCo, 6 ABO_r); *Old Crow, 19-VII-1977 (1 ABO_r).

UNITED STATES

ALASKA: Mi. 6 (Km 10), McKinley, 14-VI-1954 (1 USNM); Mi. 13.5 (Km 21.7) Cantwell Rd., 17-VI-1954 (1 USNM).

Third Instar Larvae

ALBERTA: 1.5 mi. (2.4 km) W. Edmonton, 26-V-1975 (8 ABO_r, 4 UASM); 1 mi. (1.6 km) S. Jasper, 4-VI-1975 (5 ABO_r, 5 CNC, 4 UASM); 20 mi. (32 km) W. Edson, 29-V-1976 (3 ABO_r, 2 CNC, 2 UASM); 0.9 mi. (1.4 km) W. George Lk., 12-V-1975 (8 ABO_r, 3 UASM); NORTHWEST TERRITORIES: Pond nr. Harris River, 2-VI-1973 (1 CNC); YUKON TERRITORY: Klutlan Glacier moraine, VII-1971 (6 EFCo).

Second Instar Larvae

ALBERTA: 1 mi. (1.6 km) S. Jasper 25-VI-1976 (3 ABO_r); 7 mi. (11 km) E. Obed, 27-IV-1976 (8 ABO_r, 4 UASM); 20 mi. (32 km) W. Edson, 27-IV-1976 (4 ABO_r, 4 UASM); 0.9 mi. (1.4 km) W. George Lk., 24-IV-1976 (8 ABO_r, 4 UASM).

First Instar Larvae

ALBERTA: 1 mi. (1.6 km) S. Jasper 25-IV-1976 (8 ABO_r, 4 UASM); 20 mi. (32 km) W. Edson, 27-IV-1976 (4 ABO_r, 4 CNC).

Eggs

From male and female adults collected as fourth instar larvae 0.9 mi. (1.4 km) W. George Lk., Alberta and reared and mated in laboratory (ABor).

*Material identified but not measured.

Taxonomic notes. – Because many specimens of *Chaoborus cooki* key out to *Chaoborus nyblaei* using Saether's (1972) keys, records of *Chaoborus nyblaei* by Anderson and Raasveldt (1974) probably refer to specimens of *Chaoborus cooki*. The numbers of anal fan setae and PAL/PAW recorded by Smith (1960b) suggests that *Chaoborus cooki* larvae were examined. The suggestion by James and Smith (1958) that some of the *Chaoborus nyblaei* population overwinters in the egg stage at Churchill, Manitoba, indicates the presence of *Chaoborus cooki*.

The only previous description of *Chaoborus cooki* is that of the adults, pupae and fourth instar larvae by Saether (1970). Cook (1956) undoubtedly included specimens of *Chaoborus cooki* in his description of *Chaoborus nyblaei*. The larval head capsule length recorded by Cook (1956) as 2.78 mm, larger than any recorded here, probably refers to a specimen of *Chaoborus cooki*. Contrary to Saether's (1970: 26) statement, Cook's (1956) description of the abdomen probably included *Chaoborus cooki*.

Saether (1970: 20) incorrectly states that *Chaoborus cooki* larvae do not have a dorsal process on abdominal segment IX (see page 157).

Chaoborus nyblaei (Zetterstedt)

Erioptera nyblaei Zetterstedt 1838: 830. Three syntypes, all females; LECTOTYPE HERE DESIGNATED, labelled: 'Corethr. nyblaei, Z. ♀, Erioptera, (illegible word), Lapp Dovre'; one syntype with no label and the other labelled 'Corethr. nyblaei, Z. ♂, Erioptera, (illegible word) Lapp Dovre.'; (ZMLS).

Corethra nyblaei; Zetterstedt 1851: 3794. Giles 1902: 502. Theobald 1901b: 291.

Chaoborus nyblaei; Edwards 1930: 533. Edwards 1932: 26. Hirvenoja 1961. Saether 1970: 14, in part.

?*Corethra pilipes* Gimmerthal 1845: 297. Location of male type unknown. Collected at Riga, Latvijas S.S.R.

Description. – Males. (n=two, unless otherwise given in parentheses). Total length 7.9–8.5 mm; general body coloration light grayish brown; vittae brown; specific pigmentation as other members of subgenus.

Antennae: pedicel width 302–319 μm ; length of flagellar articles 1,2–11,12,13: 244–267 μm , 148–151 μm , 354–371 μm , 261 μm ; P/U 1.42–1.56 μm .

Head: width 1096–1125 μm ; width between eyes 313–389 μm ; clypeus length 447–464 μm ; prementum length 470–493 μm ; head width/width between eyes 2.90–3.50; head width/clypeus length 2.42–2.45; head width/prementum length 2.22–2.40; number of setae on vertex 106 (1); lengths of palpal articles two to five: 121–139 μm , 249–261 μm , 244–313 μm , 528 μm (1).

Thorax: number of setae: pronotal 24; postpronotal three or four; proepisternal seven or eight; preepisternal four to seven; anepisternals 12 or 13; upper mesepimerals 14 or 15; scutellar 72–88; supraalar 37 or 38.

Wing: length 4.53–4.63 mm; width 1.03 mm; length/width 4.41–4.51; wing length/head width 4.03–4.15; wing length/length of femur of foreleg 1.68 (1); Y/X 1.88–2.13; Y/Z 1.35–1.59; Y/R₃ 0.75–0.77; Z/M₁ 0.44–0.56; R₃/M₁ 0.94–0.99; number of setae on squama 38 (1); length of Rsa 271 μm (1).

Haltere: capitulum nearly spherical; two to three anterior setae; two to three posterior setae.

Legs: Foreleg: Fe 2690 μm (1); Ti 1251 μm (1); Ta₁ 590 μm (1); Ta₅ 249 μm (1); Hindleg: Fe 2997 μm (1). Length of foreleg claw 85 μm (1); pulvilli length 53 μm (1).

Genitalia. number of setae on tergite IX 10 (1); penis valve length 194–226 μm ; penis valve as shown in Fig. 11,0 and P; gonocoxite length 702 μm (1); gonostylus length 609–632 μm ; HR 1.15 (1); HV 1.25–1.39.

Females. (n=three, unless otherwise given in parentheses). Total length 8.0 mm (1); general body coloration light grayish brown; vittae brown; specific pigmentation as other members of subgenus.

Antennae: (n=2) pedicel width 162 μm ; length of flagellar articles 1,2–11, 12,13: 192–203 μm , 124–138 μm , 180–191 μm , 197–215 μm ; P/U 0.89–0.91.

Head. (n=2) head width 1102 μm ; width between eyes 360–400 μm ; clypeus length 464–487 μm ; prementum length 493–528 μm ; head width/width between eyes 2.75–3.06; head width/clypeus length 2.26–2.38; head width/prementum length 2.09–2.24; number of setae on vertex 134–146; length of palpal articles two to five: 151–157 μm , 290–313 μm , 302–331 μm , 586–621 μm .

Thorax. Coloration as in male.

Number of setae: pronotals 24–43; 70.0; postpronotals 3–11, 6.7; proepisternal 8–11, 9.3; preepisternal 8–10, 9.0; anepisternals 13–34, 24.0; upper mesepimerals 17–24, 19.3; scutellar 87–119, 98.3; supraalar 53–66, 59.7.

Wing. ($n=6$, unless otherwise given) coloration as other members of subgenus. length 5.5–6.3, 5.9 mm; width 1.4–1.8, 1.6 mm; length/width 3.55–4.09, 3.84; wing length/head width 5.17–5.25 (2); wing length/length of femur of foreleg 2.22–2.67 (2); Y/X 2.29–3.43, 3.10; Y/Z 1.33–1.67, 1.53; Y/R_3 0.70–0.93, 0.79; ZM_1 0.42–0.56, 0.50; R_3/M_1 0.91–1.01, 0.96; R_{5+6} 126–302, 238 μm .

Halteres: capitulum nearly spherical; two anterior setae (2); two to eight posterior setae (2).

Legs. (2), coloration as other members of the subgenus.

Foreleg: Fe 2608–2631 μm ; Ti 2761–2796 μm ; T_1 1345–1369 μm ; Ta_2 802 μm ; Ta_3 625–627 μm ; Ta_4 389–401 μm ; Ta_1/Ti 0.49.

Midleg: Fe 2395–2537 μm ; Ti 2230–2384 μm ; Ta_1 1121–1145 μm ; Ta_2 637 μm ; Ta_3 496 μm ; Ta_4 318–342 μm ; Ta_5 273–296 μm ; Ta_1/Ti 0.47–0.51; 7 setae in Ta_3 comb (1).

Hindleg: Fe 2974–3221 μm ; Ti 2620–2950 μm ; Ta_1 1758–1782 μm ; Ta_2 909–944 μm ; Ta_3 625–649 μm ; Ta_4 366–413 μm ; Ta_5 319–325 μm ; Ta_1/Ti 0.60–0.67; 7 setae in Ta_3 comb (1).

Length of foreleg claw: 94 μm ; pulvilli length 56–61 μm .

Genitalia: seminal capsule diameter 65–76; 71.4 μm ; 1.4 (4); cerci length 267–284, 274 μm (4).

Male pupae. Measurements and proportions: see Table 20.

Female pupae. Measurements and proportions: see Table 21.

Fourth instar larvae. Measurements and proportions: see Table 22.

Eggs: only eggs dissected from abdomens of females were examined. Measurements are probably not, therefore, very accurate. Eggs from lectotype with thick exochorionic layer (Fig. 9B); eggs from female from Abisko with exochorionic layer as relatively thick as that shown in Figure 9C. Sculpturing of exochorion not discernable. Measurements and proportions: see Table 23.

Bionomics. – Probably overwinters in egg stage. Larvae have been collected from both permanent and, possibly, temporary lentic habitats (Hirvenoja, 1961). This species may be able to invade temporary ponds. Adults emerge about the end of July.

Derivation of specific epithet. – Named after Olavus Nyblaeus.

Distribution. – The distribution of *Chaoborus nyblaei* is shown in Fig. 20. Although this species is known from certain records only from Fennoscandia, it may, especially if *Chaoborus pilipes* from Riga, Latvijaska S.S.R. is conspecific with *Chaoborus nyblaei*, be more widely distributed in the boreal region of the Palaearctic region. If this species has requirements similar to those of *Chaoborus trivittatus* and *Chaoborus cooki*, *Chaoborus nyblaei* is restricted to areas of boreal woodland.

LOCALITIES

Male Adults

FINLAND: 2–3 km SW Nuorgam, 24-VII-1960 (1 ZMHF); SWEDEN: Abisko, 1931 (1 BMNH).

Female Adults

FINLAND: 2–3 km SW Nuorgam, 24-VII-1960 (2 ZMHF); SWEDEN: Abisko, 1931 (1 BMNH); NORWAY: Dovre, 30-VII-? (2 ZMLS); unlabelled specimen from type series (1 ZMLS).

Male Pupae

FINLAND: 2–3 km SW Nuorgam, 24–25-VII-1960 (2 OASa; 2 ZMHF).

Female Pupae

FINLAND: 2–3 km SW Nuorgam, 24–25-VII-1960 (4 OASa; 3 CNC; 4 ZMHF).

Fourth Instar Larvae

FINLAND: 2–3 km SW Nuorgam, 24–25-VII-1960 (2 OASa, 2 CNC; 20 ZMHF; 2 ABOr).

Eggs

From females collected as follows: SWEDEN: Abisko, 1931 (1 BMNH); NORWAY: Dovre, 30-VII-? (1 ZMLS).

Taxonomic notes. – Considerable confusion has surrounded the name of this species. Edwards (1920: 265), Martini (1931: 58), and Séguy (1942: 169) incorrectly considered *Chaoborus nyblaei* to be conspecific with *Chaoborus pallidus* (Fabricius). Many authors treated *Schadonophasma* as monotypic

Table 20. Descriptive statistics for male pupae of *Chaoborus nyblaei*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean
Total abdomen length (mm)	4	5.5–5.9	5.7
Respiratory horn length (mm)	4	1.31–1.42	1.38
Respiratory horn width (mm)	4	0.30–0.38	0.33
Abdominal segment VII length	4	1003–1109	1056
Abdominal segment VII width	4	1735–1923	1808
WS/LS	4	1.63–1.74	1.71

Table 21. Descriptive statistics for female pupae of *Chaoborus nyblaei*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm)	11	6.4–7.8	7.1	0.74	0.31
Respiratory horn length (mm)	6	1.59–1.73	1.64		
Respiratory horn width (mm)	6	0.37–0.46	0.43		
Abdominal segment VII length	11	1144–1310	1223	77	31
Abdominal segment VII width	11	2030–2383	3315	167	67
WS/LS	11	1.71–1.89	1.81	0.082	0.033

Table 22. Descriptive statistics for fourth instar larvae of *Chaoborus nyblaei*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	25	1853–2596	2231	305	0.82
Antennal length	26	870–1160	1037	138	36
LB/SB	26	1.24–1.93	1.54	0.206	0.056
LB/AL	26	0.47–0.74	0.650	0.087	0.023
AS/AL	26	0.78–0.91	0.864	0.044	0.012
Postantennal filament length	26	684–1015	845	122	32
PAL/PAW	25	2.00–5.30	3.56	1.142	0.305
Number mandibular fan bristles	25	8–13	12.3	0.95	0.25
Number anal fan setae	24	34–40	36.6	2.90	0.80

Table 23. Descriptive statistics for eggs of *Chaoborus nyblaei*. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Length without exochorion	14	625–778	670	64	23
Width without exochorion	14	236–330	291	42	15
Thickness of exochorion	6	71–106	88		

or have followed Saether's (1970) conclusion that *Chaoborus nyblaei* occurs in North America and, consequently, have incorrectly applied this name to North American specimens of *Schadonophasma* (Allan, 1973; Anderson and Raasveldt, 1974; Cook, 1956; Dodson, 1970; James and Smith, 1958; James *et al.* 1969; Jenkins and Knight, 1950; Main, 1953; Maleug and Hasler, 1967; Matheson, 1944; McCloy, 1950; Myklebust, 1966; Peus, 1967; Smith, 1960b; Stahl, 1966; Teraguchi and Northcote, 1966).

The only previous detailed description of male adult *Chaoborus nyblaei*, by Saether (1970), was based on a specimen of *Chaoborus trivittatus* from Baffin Island, Canada, and the hypopygium of a specimen of *Chaoborus nyblaei* from 2–3 km SW Nuorgam, Finland. The main diagnostic character was shape of the penis valve. Reorientation of the genitalia of these specimens, however, showed that the characterization by Saether (1970) was incorrect. Penis valves of the specimen from Baffin Island are typical of *Chaoborus trivittatus*. Those from the specimen from Finland are similar to, but different from, penis valves of *Chaoborus trivittatus*. I was able to associate the hypopygium from Finland with the rest of the specimen, and the description includes this male.

Adult characters described by Saether (1970), but not given here, were those which could not be measured.

Pupae and fourth instar larvae have been previously described by Hirvenoja (1961) and Saether (1970).

Of the three syntypes of *Chaoborus nyblaei* only measurements of the female genitalia of the lectotype are included in this description. The lectotype and paralectotypes were used only to describe color and wing characters. The features of the pharate female adult prepared from a pupa and described by Saether (1970), are not included in this description.

Saether (1970: 16) incorrectly states that fourth instar larvae of *Chaoborus nyblaei* do not have a noticeable dorsal process on abdominal segment IX (see page 156).

The first, second, and third instar larvae of *Chaoborus nyblaei* are unknown.

ANALYSIS OF MORPHOLOGICAL VARIATION

The following is a discussion of morphological variation of the stages of *Schadonophasma* species. These results describe differences between species of eggs, all larval stages, pupae and adults. Interpretation of some intraspecific morphological variation as the result of age-related, sex-associated and geographical variation, and, as described for *Chaoborus trivittatus*, the result of past distributions, is also provided. Detailed study of structure, especially when combined with bionomic and behavioral observations, can allow interpretation of the functional significance of characters. These data thereby provide an enhanced means of understanding intraspecific variation and phyletic relationships. Comparison of results with studies of other *Chaoborus* species is provided to facilitate further comparison between species of *Chaoborus*, to reinterpret some past results, and to suggest, in some instances, more likely interpretation of data presented here.

Artificial variation

An important source of error in determining intraspecific and interspecific variation of species can result from methods employed in the preservation or preparation of specimens. This factor accounts for some variation previously described.

Cook (1956: 29) noted that thoracic coloration of adult males of *Schadonophasma* was related to age of pinned specimens. Ground color had changed from light grey to yellowish-brown in specimens which had been pinned for more than twenty years. I have not been able to confirm this observation which may be due, in part, to Cook's (1956) inclusion in his analysis of adults of both *Chaoborus trivittatus* and

Chaoborus cooki, which do differ in thoracic coloration. In addition, glue had seeped unto the thorax of some of the older pinned specimens producing a darker hue.

The color of all material, of any stage, appeared to bleach when preserved in ethanol for more than about four or five years. In addition, clearing with KOH also bleaches the color of specimens. It is uncertain, therefore, whether Saether (1967) adequately described the color variation of KOH-treated larvae of *Chaoborus flavicans*.

Saether (1970: 21) recognized the distinct conical dorsal process of *Chaoborus brunskilli* (= *Chaoborus trivittatus*) fourth instar larvae as diagnostic. Of all material examined, however, only fourth instar larvae preserved in formalin possessed dorsal processes similar to those of *Chaoborus brunskilli* drawn by Saether (1970: fig. 11Q,R) and ethanol-preserved material exhibited flatter dorsal processes (Fig. 2B; 8C,D). Paratype larvae of *Chaoborus brunskilli* came from two localities. Hamilton (1971) states that the specimens from near Kenora, Ontario were preserved in formalin. Anderson and Raasveldt (1974) do not mention the preservative used to kill the specimens from East Henry Pond, Jasper National Park, Alberta. Main (1953: 21) reported reduction in total length of 3.3–11.3% of 23 larvae of *Chaoborus trivittatus* or *Chaoborus flavicans* preserved for 24 hours in formalin. The pronounced dorsal process diagnostic of *Chaoborus brunskilli* is therefore probably a result of shrinkage in formalin.

Saether (1970) erroneously suggested that *Chaoborus cooki* and *Chaoborus nyblaei* fourth instar larvae do not exhibit pronounced dorsal processes. These observations were caused by coverslips compressing cleared specimens and distorting the abdomens. All uncleared fourth instar larvae of *Chaoborus cooki* subsequently examined had a developed dorsal process (Fig. 8D). Additional specimens of *Chaoborus nyblaei*, which had been cleared but preserved in fluid, were available and I mounted these under coverslips supported by glass chips. The abdomens retained their natural dimensions and this allowed observation of the developed dorsal process (Fig. 8C) similar to those of other fourth instar larvae of *Schadonophasma*.

McGowan (1976) reported six or eight postantennal filaments for second instar, and eight or ten postantennal filaments for third instar larvae of *Chaoborus edulis*. However, the larvae of *Chaoborus pallidipes* (Theobald), which are presently indistinguishable from those of *Chaoborus edulis* (compare Green and Young, 1976; McGowan, 1976), have the two posterior postantennal filaments distinctly separated (much more so than described for *Chaoborus flavicans* by Balvay (1977c)) from the rest of the filaments and, if *Chaoborus edulis* also possesses this trait, McGowan's (1976) results reflect the breaking off of this separate pair and the variation is probably an artifact of preparation.

Saether's (1970) misinterpretation of interspecific variation of penis valve shape of adult males because of lack of standard orientation of these is described elsewhere (p. 177).

Characters varying between larval instars

Hennig (1966a) has discussed the importance of making comparisons only between comparable semaphoronts in systematic work. The only difficulty in recognizing semaphoronts of *Schadonophasma* concerns the four larval instars; this section describes differences which permit recognition of each of these.

Data on instar differences also allowed comparison of developmental patterns from instar to instar between species and, for some characters, provided important clues for determining the polarity of morphoclines for phyletic studies.

Differences between instars of *Chaoborus* have been described by Balvay (1977a, 1977b, 1977c), Deonier (1943), Fedorenko and Swift (1972), Green (1972), MacDonald (1956), Maleug (1966), McGowan (1972, 1976), Parma (1969, 1971a), Prokesova (1959), Saether (1967, 1970), Sikorowa

(1967b, 1970, 1973), Smith (1960a), Teraguchi and Northcote (1966), von Frankenberg (1915), and Weismann (1866). Few workers have considered geographical variation in their analysis of instar differences (Balvay, 1977a, 1977b, 1977c; Green 1972; Saether, 1967, 1970: 22; Sikorowa, 1973).

Sikorowa (1973) showed that *Chaoborus flavicans* larvae collected from ponds or lakes differed significantly in a number of characteristics, suggesting that ecological factors produce at least some variation. One character, the length of the longest antennal blade, differed significantly between first instar larvae collected from these two habitat types, implying genetic differences.

It was not previously known, therefore, what characters could be used with certainty to distinguish instars of material collected over an extensive geographical area, and an extensive range of habitats. This paper provides that information for larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Although some mistaken interpretations of characters are discussed here, qualitative differences between instars are given in the description of *Chaoborus* and are not repeated here.

Mensural characters previously found to differ between instars, but not necessarily without some overlap of variation, were total length, distance between anterior and posterior air sacs, head capsule length, antennal length, distance of antennal seta from base of antenna, long antennal blade, short antennal blade length, AS/AL, LB/SB, postantennal filament length, PAL/PAW, number of mandibular fan bristles, and number of anal fan setae. Total length and distance between anterior and posterior air sacs were not measured because they are clearly related to growth and exhibit continuous variation (Balvay, 1977b; Eggleton, 1932; Fedorenko and Swift, 1972; Hongve, 1975; LaRow and Marzolf, 1970; Lewis, 1975; MacDonald, 1956; Main, 1953; Malueg, 1966; McGowan, 1972; Parma, 1971a; Saether, 1967; Sikorowa, 1973; Smith, 1960a; Teraguchi and Northcote, 1966).

Smith's (1960a) report that *Chaoborus crystallinus* first instar larvae have six terminal antennal setae is probably erroneous. Sikorowa (1973: fig. 13) shows only four setae. Further differences between first instar *Chaoborus flavicans* as described by Parma (1971a) and first instar *Chaoborus crystallinus* as described by Smith (1960a) suggest that some second instar larvae contaminated Smith's (1960a) sample of first instar larvae.

Homologous structures in first and later larval instars of Schadonophasma. – To accurately depict differences between larval instars, homologous structures should be compared. Failure to do so has led to nomenclatural misinterpretation of certain structures in the past.

There has been confusion concerning the setae of the mandible of first instar larvae of *Chaoborus*. Parma (1971a: 178) suggests that *Chaoborus flavicans* first instar larvae exhibit a mandibular fan composed of three setae, but Sikorowa (1967b: 88) mentions the presence of four setae. *Chaoborus astictopus* first instars do not have a mandibular fan (Deonier, 1943:385). Saether (1970: 22) states that *Chaoborus brunskilli* (= *Chaoborus trivittatus*) first instar larvae have a mandibular fan of nine bristles. Reexamination of specimen showed a mandible typical of first instars (Fig. 8A) and suggests that the mandibular fan bristles counted were those of the pharate second instar which was present.

All first instar material examined exhibited mandibles similar to that in Figure 8A (also Balvay, 1977c: fig. 4; Weismann, 1866: fig. 22A).

The homologies of mandibular structures of *Chaoborus* larvae, as considered by all authors, are summarized in Table 24.

Balvay (1977c) discusses at length the nomenclature of the mandible of different instars of *Chaoborus flavicans*, and gives new names for all structures except the mandibular fan. He showed that the mandibles of second, third, and fourth instar larvae were structurally similar to each other but were all different from first instar larval mandibles. Balvay (1977c) considered the "mandibular fan" of first instar larvae to be composed of three setae, and to be homologous to the mandibular fan of later instars, but does not give any justification for doing so. A fourth articulated seta between the teeth of the

Table 24. Comparison of studies of homologies of mandibular structure of larvae of *Chaoborus*.

First Instar Larvae			Later Instar Larvae		All Instars
Balvay, 1977c	Parma, 1971a	Sikorowa, 1967b	Knight, 1971b	Balvay, 1977c	This study
Mandibular fan	Mandibular fan	Mandibular fan	Mandibular spurs	Mandibular setae	Mandibular spurs
Mandibular seta	Mandibular tooth				
Spines E ₁ , E ₂	(not reported)	(not reported)	Mandibular spur	Spines E ₁ ,E ₂	Seta O–MP unnamed seta
			Mandibular comb and brush	Mandibular fan	Mandibular fan

mandible and the “mandibular fan” was considered homologous to one of the mandibular setae (=mandibular spur of Knight, 1971b) of later instars. Mandibular setae of the second instar developed at the base of the mandibular seta of the first instar larval mandible. In addition, a nerve extends from the mandibular seta base in the first instar to the bases of the two mandibular setae of the second instar. The mandibular seta of the first instar larval mandible identified by Balvay (1977c) is therefore clearly homologous to one of the mandibular setae of later instars.

Although Balvay (1977c) mentions that the mandibular setae of the pharate second instar larva cannot develop inside the first instar mandibular seta because of the basal articulation, the tips of the mandibular fan bristles of pharate second instar larvae of both *Chaoborus trivittatus* and *Chaoborus cooki* do develop inside this mandibular seta.

Mandibles of first instar larvae of *Chaoborus* are similar to those of *Mochlonyx* (James, 1957: fig. 9) which possess four (only three shown by James) setae, three of which are toothed and are very similar and probably homologous to those of later instars of *Mochlonyx* (Cook, 1956: fig. 22E; Johannsen, 1934: fig. 155; Meinert, 1886: 65). However, mandibles of second, third and fourth instar larvae of *Mochlonyx* also bear mandibular fans undoubtedly homologous to the mandibular fans of *Chaoborus*. The three setae on the mandible of first instar *Chaoborus* larvae are therefore not homologous with the mandibular fan of later instars as suggested by Balvay (1977c), Parma (1971a), Sikorowa (1967b, 1973), and Smith (1960a); they are mandibular spurs (Knight, 1971b). Only two of the mandibular spurs, each with a similar pointed mandibular projection at their base, as all four setae of first instars, are retained by later instars. I am not certain that the naming of the mandibular fan as the mandibular brush and comb by Knight (1971b) is justified. I therefore retain the traditional name.

One of two additional setae on the mandible of first instar *Chaoborus* larvae (Fig. 8A), called spines E₁ and E₂ by Balvay (1977c), is probably homologous with seta O-MP (Knight, 1971b) of some culicid larvae. Both setae are retained in later instars of *Chaoborus* (Fig. 8B; Balvay, 1977c: fig. 5,6,7). The setae are undoubtedly homologous to the two setae on the mandible of first instar *Mochlonyx* (James, 1957: fig. 9) and *Eucorethra underwoodi* Underwood (pers. obs.) larvae. Also present in later instars of *Mochlonyx*, these two setae are retained in later instars of *Eucorethra underwoodi* where they are labelled as the pectinate brush by Knight (1971b: fig. 1d). However, their placement, and similarity to

those of the mandible of *Chagasia bathana* (Culicidae) (Knight, 1971b: fig. 2f), suggests one of these is seta O-MP. I therefore label the large seta on the mandible of later instars of *Chaoborus* as such, although it is not certain which of the two is actually seta O-MP. Knight (1971b) does not label the second seta. Knight (1971b: fig. 1e,f) incorrectly labelled seta O-MP as one of the mandibular spurs on the mandible of *Chaoborus americanus* (incorrectly identified as *Chaoborus flavicans*).

Sikorowa (1967b: fig. 1a,b) erroneously shows both second and fourth instar larvae of *Chaoborus flavicans* with three mandibular spurs.

Previous authors have misinterpreted changes in the anal fan between first and second instar larvae. Balvay (1977b) considered, without justification, each pair of anal fan setae of first instar larvae to correspond to a single anal fan seta of the second instar. Sikorowa (1970) mentions that these pairs of setae arise from a common base. This is not so in any of the material I have examined, but the sockets for the two setae are placed laterally very close to one another. This paired arrangement of setae is reflected in all later instars in which, although the setae are in an anterior-posterior plane (Fig. 2B), all anal fan setae are placed alternately slightly one side or the other of the sagittal plane. This, and the fact that the number of anal setae for first and second instar larvae is nearly identical for both *Chaoborus trivittatus* and *Chaoborus cooki*, supports the view that each seta in the first instar corresponds to a single seta in the second instar.

Head capsule length. – Variation in this measurement is useful to distinguish *Chaoborus* larval instars (Fedorenko and Swift, 1972; Goldspink and Scott, 1971; LaRow and Marzolf, 1970; Malueg, 1966; MacDonald, 1956; Parma, 1969, 1971a; Prokesova, 1959; Saether, 1967, 1970; Sikorowa, 1973; Teraguchi and Northcote, 1966; von Frankenberg, 1915). However, Balvay (1977c) found that the range of head capsule length overlapped between third and fourth instar larvae of *Chaoborus flavicans*. Variation in lengths of larval head capsules of *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 21A) shows, consistent with most previous work, no overlap of range between any of the instars within each species, although ranges of third and fourth instar *Chaoborus trivittatus* are proximate. Head capsule length is sex-associated in fourth instar larvae and therefore probably in third instars and any overlap between these instars, as shown by Balvay (1977b), is probably due to a mixture of male fourth instar and female third instar larvae.

Antennal length. – Antennal length is useful to discriminate all instars (or at least 99% of all specimens when authors do not give ranges) collected at a single locality or in a limited geographical region (Green, 1972; McGowan, 1972, 1974, 1976; Parma, 1971a; Saether, 1970; Sikorowa, 1973). Saether (1967) reported a slight overlap between third (330–420 μ m) and fourth (420–640 μ m) instar antennal lengths of *Chaoborus flavicans* samples from throughout this species' range. Balvay (1977b) reported overlap of antennal lengths only between second and third instars of this species collected in France. Range of variation for *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 21B) shows that this character can be used to discriminate all instars. Like head capsule length, to which this character is correlated at least in male larvae, antennal length of third and fourth instar *Chaoborus trivittatus* larvae overlap slightly. As this character also exhibits sex-associated variation in fourth instar larvae, the proximity between antennal lengths of third and fourth instar larvae is probably due in part to this source of variation. This, however, could not fully explain Balvay's (1977b) finding of overlap between second and third instars only.

Distance of antennal seta from base of antenna/antennal length (AS/AL). – Parma (1971a: 177) for *Chaoborus flavicans*, and Saether (1970: 22) for *Chaoborus brunskilli* (= *Chaoborus trivittatus*), showed that differences in AS/AL distinguish all instars, although Balvay (1977b) showed overlap for each instar of *Chaoborus flavicans*. *Chaoborus trivittatus* and *Chaoborus cooki* overlap between second and third, and between third and fourth instars (Fig. 22A). Later instars of *Chaoborus trivittatus*

exhibit, particularly between second and third instars, a substantial degree of overlap of range of AS/AL. Therefore this character is useful to distinguish all first instar larvae and only some second, third and fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Change in the ratio from instar to instar is more constant in *Chaoborus cooki* than in *Chaoborus trivittatus*, where there is a more pronounced increase from first to second, and a lesser increase from second to third and third to fourth instars.

Length of long antennal blade/antennal length (LB/AL). – This ratio distinguishes all first instar larvae of *Chaoborus cooki* and all first and second instars of *Chaoborus trivittatus* from all later instars (Fig. 22B). The character can also be used to distinguish some fourth from third instar larvae of *Chaoborus trivittatus* and some second, third and fourth instar larvae of *Chaoborus cooki*.

Length of long antennal blade/length of short antennal blade (LB/SB). – First instar larvae do not possess the short antennal blades of later instars. Inequality of length of antennal blades noted by Balvay (1977b) and Parma (1971a: 176) for first instar larvae of *Chaoborus flavicans* is also present in later instars where one of the long antennal blades is slightly shorter than the other three. Both Balvay (1977b) and Parma (1971a: 177) have shown that, although there were statistical differences between LB/SB of second, third and fourth instars of *Chaoborus flavicans*, there was a good deal of overlap of range. Saether (1967: Table 1) showed overlap of variation of this ratio between third (0.43–0.64) and fourth (0.50–0.60) instar larvae of *Chaoborus flavicans*.

Considerable overlap is exhibited between second, third and fourth instars of *Chaoborus brunskilli* (= *Chaoborus trivittatus*) (Saether, 1970: 22). LB/SB overlaps in range between the last three instars of both *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 23A). There were differences in the pattern of change of LB/SB from instar to instar between *Chaoborus trivittatus* and *Chaoborus cooki*. At least some individuals of *Chaoborus cooki* can be identified to instar using this character where the ratio decreases with each successive instar. The range of ratio for the three later instars of *Chaoborus trivittatus*, however, are nearly identical to each other. There is only a slight increase in the means of the ratio between second and third instars and a slight decrease between third and fourth instars.

As antennal blades are undoubtedly important in capture and ingestion of prey, differences in progression of prey type from instar to instar between *Chaoborus trivittatus* and *Chaoborus cooki* may be suggested. However, detailed interpretation of the adaptive significance of this difference must await further study. *Chaoborus trivittatus* larvae (Fedorenko, 1975a, 1975b; Swift, 1976; Swift and Fedorenko, 1975) probably show closer affinities in prey selection to *Chaoborus flavicans* larvae (Berg, 1937; Dodson, 1970; Parma, 1971b: 43; Sikorowa, 1973: Table 18; Swüste *et al.* 1973) which exhibit allometric change in LB/SB similar to that of *Chaoborus cooki*. However *Chaoborus cooki*, because of the temporary ponds it inhabits, takes quite different types of prey (commonly ostracods, chironomid larvae, culicid larvae). Therefore, an explanation of differing food types does not adequately explain the differences in the pattern of change of LB/SB in *Chaoborus trivittatus* and *Chaoborus cooki*.

Postantennal filaments. – Parma (1971a), Saether (1967, 1970) and Sikorowa (1973) showed no overlap of range between instars in postantennal filament length.

Results for *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 23B) show that this character is useful to distinguish all individuals of each instar of *Chaoborus cooki* and all, except a few (due to one specimen each) third and fourth *Chaoborus trivittatus*. The smallest antennal filament length of fourth instar larvae is from specimens collected 85 km north of Coleman, Alberta from a high altitude (1975 m) pond which was not shaded. The extreme environmental conditions of this habitat possibly results in smaller individuals.

Prelabral appendages. – Parma (1971a: 176), Saether (1967: Table 1; 1970: 22) and Sikorowa (1973: fig. 9) have shown, in *Chaoborus* species with laterally flattened prelabral appendages in third

and fourth instar larvae, that generally prelabral appendages of third instar larvae are more slender than are those of fourth instar larvae. This is also true for these instars of *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 24A). Amount of overlap of PAL/PAW between third and fourth instar larvae is especially pronounced for *Chaoborus trivittatus*.

Number of mandibular fan bristles. – This character is useful to identify all specimens to instar in only a few species (Balvay, 1977b; Deonier, 1943; Green, 1972; McGowan, 1972, 1976; Parma, 1971a; Saether, 1967; Sikorowa, 1967b; 1973).

There is some overlap of range in number of mandibular fan bristles between second, third, and fourth instar larvae of both *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 24B) and this character alone can be used only to recognize some second and fourth instars of either *Chaoborus trivittatus* or *Chaoborus cooki*. Range of number of mandibular fan bristles increases in successive instars at a greater rate in *Chaoborus trivittatus* than in *Chaoborus cooki*.

Anal fan setae. – Differences in number of anal fan setae between larval instars have been described for some *Chaoborus* species by Balvay (1977b). Deonier (1943), McGowan (1972, 1976), Parma (1971a), Saether (1967, 1970), Smith (1960a) and Sikorowa (1973).

Variation of this character for *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 25A) shows that only some fourth instar larvae of either *Chaoborus trivittatus* or *Chaoborus cooki* can be distinguished using the number of anal fan setae. First instar larvae may be distinguished from second instar larvae by their paired arrangement of setae (Balvay, 1977b; Parma, 1971a; Sikorowa, 1970, 1973).

Variation of characters of fourth instar larvae

Age-related variation. – Age-related variation of fourth instar larvae was studied for *Chaoborus cooki* only. These were collected 1.6 km south of Jasper on June 4 (n=29) and June 17, 1975 (n=33) with third instar larvae and pupae, respectively. This ensured a sample of fourth instar larvae which exhibited the total age range. Total length was interpreted as representative of age, and statistical correlation of the following characters with total length was studied to determine age related variation: antennal length, long antennal blade length, short antennal blade length, LB/SB, LB/AL, distance of antennal seta from antennal base, AS/AL, postantennal filament length, prelabral appendage length and width, PAL/PAW, number of mandibular fan bristles and number of anal fan setae. Shape of dorsal process was also studied.

Male and female larvae were distinguished using the index described below in the section about sex-associated variation. Probably because of small sample size, female larvae exhibited no characters significantly correlated with body length. Three characters of male larvae were significantly negatively correlated with growth: long antennal blade length, LB/AL, and prelabral appendage length. Because long antennal blade length and antennal length are not correlated to each other in male larvae, the correlation of LB/AL to total length probably reflects the correlation of the long antennal blades to total length. Therefore only two remaining characters are meaningfully related to age. Relationship to total length of both long antennal blade length (Fig. 26A) and prelabral appendage length (Fig. 26B) indicates wear with age of these two structures. Wear of long antennal blade is probably associated with prey capture. Roth (1967: 66) previously noted wear of prelabral appendages of overwintered *Chaoborus albatus* larvae. Evidence of damage, particularly to the tip of prelabral appendages, producing a blunt tip and therefore a shorter prelabral appendage, is common in fourth instar larvae of *Chaoborus trivittatus* (Fig. 13G), *Chaoborus cooki* and *Chaoborus nyblaei* (Fig. 15A-D). Examination of freshly captured, fluid-preserved material shows that wear of the prelabral appendages is not an artifact of preparation.

Although the drawing of the prelabral appendage of *Chaoborus nyblaei* by Saether (1970: fig. 11G)

does not show it, the tip had been broken off and the prelabral appendages of *Chaoborus nyblaei* fourth instar larvae are in fact more elongate (Fig. 15E-H; Hirvenoja, 1961: fig. 2A). The breaking off of the tip of the prelabral appendages of *Chaoborus trivittatus* and *Chaoborus nyblaei* makes them appear similar to those of *Chaoborus cooki* (compare Fig. 15C, 14A-L). However, an undamaged prelabral appendage of *Chaoborus cooki* can be separated from damaged ones of *Chaoborus trivittatus* or *Chaoborus nyblaei* through examination of the form of the tip.

Sex-associated variation. – Inclusion of two different groups of semaphoronts in an analysis of variation of characters can result in an overestimation of the amount of intraspecific variation. Characters which display a large degree of sex-associated variation may therefore be mistakenly interpreted as exhibiting a greater degree of intraspecific variation than is actually present, as shown by the following analysis of some characters of fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*.

Little has been previously reported about larval sex-associated variation of *Chaoborus* species (Bradshaw, 1973: 1249; Smith, 1960a: 198, von Frankenberg, 1915: 514). Teraguchi and Northcote (1966: fig. 2) give the distribution of head capsule lengths of fourth instar larvae of *Chaoborus flavicans* collected in September which exhibits a bimodality. If this represents male and female larvae, as might be suggested by the results presented below, a comparison of the larvae collected in August and September would suggest that male larvae molt to fourth instar earlier than do females.

Chaoborus trivittatus. Statistical comparison of 14 characters (Table 25) of 23 male and 21 female larvae exuviae from reared fourth instars collected 2.4 km west of Edmonton, Alberta, April 26, 1975, indicated that eight characters differed significantly between male and female fourth instar larvae but none without some overlap.

To sex larvae without rearing, I constructed a compound character index (Table 26) in which range of variation of head capsule length, antennal length, AS/AL, long antennal blade length, LB/SB, and postantennal filament length were divided into numbered units, with typical male larvae given the lowest unit values, and female larvae the highest. Summation of values of each character for each individual showed that male and female larvae can be distinguished if the range of variation of each character in the index is divided into ten units (Fig. 27A). The method, however, depends on a large enough sample to express the bimodality.

Chaoborus cooki. Fourth instar larvae of *Chaoborus cooki* were collected 32 km west of Edson, Alberta on June 5, 1975 and reared to adulthood. Of these, 15 male and nine female larval exuviae were measured for 14 characters and statistically compared (Table 27). Five characters differed significantly between male and female larvae with only postantennal filament length showing no overlap of range. Because of proximity of ranges of postantennal filament length of male and female larvae, this character cannot be used alone to sex larvae which have not been reared. A compound character index, similar to that described above, was used to sex larvae (Table 28). Distance of antennal seta from antennal base was not used in the index because it is so markedly correlated to antennal length (Fig. 29B). Resultant index values for individual larvae (Fig. 27B) show that larvae can be sexed using this method. Fourth instar larvae used to study growth related variation were also sexed using a compound character index (Table 29). Results (Fig. 27C) were tested by examining distribution of characters used to sex larvae. For example, length of postantennal filaments over-lapped only by one specimen between male and female larvae.

It may have been due to smaller sample size used in the analysis of *Chaoborus cooki* that some characters were sex-associated for *Chaoborus trivittatus* larvae, but not for those of *Chaoborus cooki*.

Chaoborus nyblaei. I did not have reared material of *Chaoborus nyblaei* and was, therefore, unable to calculate sex-associated variation from fourth instar larvae of known sex. I attempted to sex the larvae

Table 25. Descriptive statistics for male and female fourth instar larval exuviae of *Chaoborus trivittatus* collected 2.4 km west of Edmonton, Alberta. Measurements in μm .

CHARACTER	MALES					FEMALES				
	N	Range	Mean	1.5SD	2SE	N	Range	Mean	1.5SD	2SE
Antennal Length	23	795–899	836	35	10	21	876–1003	935	44	13
Long Antennal Blade Length	23	609–696	660.9	35.4	9.8	21	673–777	723.1	42.3	12.3
Short Antennal Blade Length	23	278–365	321.8	38.5	10.7	21	290–360	324.8	30.4	8.9
LB/SB	23	1.83–2.45	2.06	0.25	0.07	21	2.04–2.52	2.23	0.19	0.06
LB/AL	23	0.68–0.84	0.791	0.053	0.015	21	0.72–0.84	0.773	0.43	0.012
Antennal Seta from Antennal Base	23	702–813	742	37	10	21	783–922	840	49	14
AS/AL	23	0.87–0.91	0.887	0.019	0.005	21	0.86–0.92	0.899	0.024	0.007
Postantennal Filament Length	23	720–791	759	34	9	21	767–885	816	53	12
Prelabral Appendage Length	23	284–447	376.0	70.5	19.6	21	261–464	367.1	82.6	24.0
Prelabral Appendage Width	23	64–87	75.2	10.6	3.0	21	70–93	81.5	12.4	3.6
PAL/PAW	23	3.27–7.00	5.06	1.34	0.37	21	2.81–6.42	4.56	1.39	0.40
Number Anal Fan Setae	23	25–29	27.4	1.4	0.4	21	25–29	27.6	1.6	0.5
Number Mandibular Fan Bristles	23	20–28	22.5	2.6	0.7	21	19–25	22.7	2.4	0.7
Head Capsule Length	20	1676–2100	1949	156	46	19	1900–2313	2116	188	57

by assuming that those larval characters exhibiting sex-associated variation for both *Chaoborus trivittatus* and *Chaoborus cooki* were also sex-associated for *Chaoborus nyblaei* larvae and constructing a compound character index similar to that for the larvae of *Chaoborus trivittatus* and *Chaoborus cooki*, on the basis of head capsule length, antennal length, long antennal blade length, and postantennal filament length. Presumably because of small sample size (n=24) I could not confidently interpret the slight bimodality present in resultant index values.

Table 26. Compound character index used to sex fourth instar larvae of *Chaoborus trivittatus* collected 2.4 km west of Edmonton, Alberta. Measurements in μm . (– = no data)

CHARACTER	INDEX VALUE									
	1	2	3	4	5	6	7	8	9	10
Antennal length	791- 815	816- 840	841- 865	866- 890	891- 915	916- 940	941- 965	966- 990	991- 1015	1016- 1040
Long antennal blade length	600- 618	619- 636	637- 654	655- 672	673- 690	691- 708	709- 726	727- 744	745- 762	763- 780
LB/SB	1.82- 1.89	1.90- 1.97	1.98- 2.05	2.06- 2.13	2.14- 2.20	2.21- 2.28	2.29- 2.36	2.37- 2.43	2.44- 2.51	2.52- 2.59
AS/AL	0.86	0.87	–	0.88	–	0.89	0.90	–	0.91	0.92
Postantennal filament length	700- 720	721- 740	741- 760	761- 780	781- 800	801- 820	821- 840	841- 860	861- 880	881- 900
Head capsule length	1676- 1741	1742- 1806	1807- 1871	1872- 1936	1937- 2001	2002- 2066	2067- 2131	2132- 2195	2196- 2261	2262- 2326

Correlation of characters. – Analysis of correlation of characters gives important clues on how best to interpret sources of variation, results of compound character indices, and characters used in phylogenetic analysis. Ratios which are significantly correlated to another ratio with which they share one character, or to one of the characters from which the ratio is composed are presented, but most of these correlations are probably artifacts of analysis (Atchley *et al.*, 1976).

Characters of male and female larvae were analyzed separately; this precluded use of specimens of *Chaoborus nyblaei*. However, characters which were significantly correlated for male and female larvae of both *Chaoborus trivittatus* and *Chaoborus cooki* were studied for *Chaoborus nyblaei* fourth instar larvae. Characters were considered significantly correlated at the 95% confidence limit. Because of low numbers of female *Chaoborus cooki* larvae studied, significance or lack of significance may be fortuitous in some comparisons.

The *Chaoborus cooki* larvae that were studied for age-related variation and *Chaoborus trivittatus* larvae that were used to determine sex-associated variation, were studied in this analysis. In addition, the *Chaoborus cooki* larvae studied for sex-associated variation were used to confirm the results from the aforementioned *Chaoborus cooki* larvae. However, presumably because of their greater numbers, some characters were significantly correlated for the *Chaoborus cooki* larvae used to determine age-related variation but were not so for the larvae used to study sex-associated variation.

Results for male and female fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki* are given in Figure 28A-D. As for *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 29A,B), distance of

Table 27. Descriptive statistics of male and female fourth instar larval exuviae of *Chaoborus cooki* collected 32 km west of Edson, Alberta. Measurements in μm .

CHARACTER	MALES					FEMALES				
	N	Range	Mean	1.5SD	2SE	N	Range	Mean	1.5SD	2SE
Antennal Length	15	945-1079	1025	67	23	9	1067-1195	1143	66	29
Long Antennal Blade Length	15	487-603	539.4	39.2	13.5	9	551-597	569.0	22.8	10.1
Short Antennal Blade Length	15	354-429	395.6	35.4	12.2	9	377-441	407.9	28.8	12.8
LB/SB	15	1.14-1.51	1.37	0.15	0.05	9	1.36-1.54	1.40	0.09	0.04
LB/AL	15	0.47-0.58	0.527	0.050	0.017	9	0.47-0.56	0.501	0.045	0.020
Antennal Seta from Antennal Base	15	812-951	873	59	20	9	905-1021	907	56	25
AS/AL	15	0.80-0.88	0.851	0.039	0.014	9	0.82-0.88	0.848	0.025	0.011
Postantennal Filament Length	15	649-802	769	61	21	9	826-885	851	29	13
Prelabral Appendage Length	15	206-294	251.2	28.4	9.8	8	229-306	268.2	43.6	20.6
Prelabral Appendage Width	15	59-100	81.9	16.5	5.7	8	71-94	84.5	11.5	5.4
PAL/PAW	15	2.29-4.30	3.13	0.79	0.27	8	2.62-3.43	3.18	0.47	0.22
Number Anal Fan Setae	13	31-36	32.6	2.3	0.9	9	32-35	33.7	1.8	0.8
Number Mandibular Fan Bristles	15	10-15	12.5	1.6	0.5	9	12-14	13.1	1.2	0.5
Head Capsule Length	15	2030-2266	2121	103	36	9	2254-2466	2373	102	45

antennal seta from antennal base is strongly correlated to antennal length of fourth instar larvae of *Chaoborus nyblaei* (Fig. 29C).

Correlation between two characters does not necessarily imply a genetic or functional relationship between those characters. However, lack of correlation suggests little relationship, and I have used only that information in subsequent analyses.

Geographical variation. – Study of geographical variation of characters of fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki* explained some of the large intraspecific variation of some characters, and provided evidence for inferring past distributions. In addition, geographical variation can give supportive evidence of reproductive isolation. Discovery of differences in patterns of geographical variation of head capsule length, AS/AL, and number of mandibular fan bristles supports the conclusion from other analyses, that *Chaoborus trivittatus* and *Chaoborus cooki* are different species.

It is difficult to determine to what extent clines are products of past and present gene flow or environmental gradients. However, analyses of intrapopulational correlation show which characters are associated, and study of patterns of geographical variation in different areas can indicate which characters are selected independently. Characters such as these, which in some locations show common patterns, are most likely to reflect gene flow and, possibly, historic events.

The geographical variation of seven characters was studied. However, because head capsule length is correlated with antennal length, at least in male larvae, and analysis of antennal length variation showed almost exactly the same pattern as head capsule length for both *Chaoborus trivittatus* and *Chaoborus cooki*, only results of variation of head capsule length are discussed here. Other characters are those used in the compound character index (Fig. 43).

Chaoborus trivittatus. I studied 21 samples from Alberta and 14 samples, or grouped samples, from the rest of North America. Within Alberta, only two areas showed geographical patterns of variation for some of the characters. The samples, numbered 1–5 and 6–9 (Fig. 30), were collected from an area near to or east of Jasper and north of Swan Hills, respectively.

The characters which show a common pattern are head capsule length (Table 30), AS/AL (Table 31), PAL/PAW (Table 32) and number of mandibular fan bristles (Table 33). Generally there is a linear increase or decrease in mean values of samples 1–5 or 6–9, corresponding to the generally linearly arranged set of localities from which samples were collected. The PAL/PAW of samples 1 and 6 do not fit the pattern suggested by other samples or other characters. In addition, direction of clines differs between areas for different characters. Mean values for head capsule length and AS/AL decrease in a west-east direction in the Jasper area and in a north-south direction in the Swan Hills area, while mean number of mandibular fan bristles decreases and PAL/PAW increases in a west-east direction in the Jasper area and south-north direction in the Swan Hills area. While reflecting gene flow, this pattern suggests the non-correlation of local selection of these two character pairs. Lack of patterns of variation of these four characters, particularly in southwestern Alberta (6 samples), is probably due to either a complicating factor or lack of resolution.

Study of six samples, or clumped samples, from Ontario, Quebec, Newfoundland, Wisconsin and Michigan indicated no apparent patterns of geographical variation, probably because of the few numbers of samples studied from such a large area.

I could distinguish no patterns of geographical variation of head capsule length for samples from outside of Alberta but, because this character can vary markedly in a relatively small area, as shown above, this was probably due to a small number of samples. Therefore it may be significant that, of all samples studied, specimens from Klutlan Glacier moraine, Yukon exhibited the highest mean head capsule length (2157 μm).

Two characters, LB/SB and number of anal fan setae, did not exhibit geographical patterns within

Alberta but did vary geographically on the west coast of North America. At least for number of anal fan setae this discrepancy is explained by the overall homogeneity of samples from Alberta which exhibit, for example, a total range of means in the Jasper region of 27.5–28.1.

Patterns of geographical variation are apparent along the west coast of North America for AS/AL (Table 34), LB/SB (Table 35), PAL/PAW (Table 36), number of mandibular fan bristles (Table 37), and number of anal fan setae (Table 38). Samples are numbered 1–7 (Fig. 31).

Variation in number of mandibular fan bristles and number of anal fan setae, exhibit a linear north-south cline with mean values increasing in a northerly direction. The number of anal fan setae of sample 6 (Table 38) is unexpectedly high, however. The other three characters, AS/AL, LB/SB, and PAL/PAW, show a different pattern of variation, with the highest mean values near the middle of the cline in the Washington or southwestern British Columbia region. None of these three characters show any intrapopulation correlation. In addition, study of AS/AL and PAL/PAW in Alberta shows that at least these two characters are independently selected for. Thus, concurrent patterns of geographical variation of these three characters probably reflect the historic events discussed below.

It seems likely, considering the present distribution of *Chaoborus trivittatus*, that this species was able to survive in both the Alaskan-Yukon refugium, and refugia south of the continental ice sheet during the Wisconsin glaciation. Because *Chaoborus trivittatus* is now restricted to woodland conditions (p. 140), discovery of woodland in parts of the Beringian refugium (Hopkins, 1972) would also suggest that *Chaoborus trivittatus* could have survived in this region.

This inferred distribution during the Wisconsin glaciation adequately explains some geographic variation. Even if an ice free corridor was present in Alberta (Reeves, 1973) and the Alaskan-Yukon refugial population was not reproductively isolated from some populations south of the continental ice sheet, this would not affect the argument presented here. Geographical patterns of variation along the west coast of North America would be the result of resumed reproduction between northern and southern populations along the west coast as the continental ice retreated (Prest, 1969).

The Yukon sample, from a pond on Klutlan Glacier moraine, exhibits the extreme of clinal variation of five characters (AS/AL, LB/SB, PAL/PAW, number of mandibular fan bristles, number of anal fan setae). These patterns are consistent with an hypothesis suggesting the past isolation of this population (see below).

Johnson (1977) has recently suggested that coastal California had a climate during the last continental glaciation similar to that now prevailing. There is little doubt that *Chaoborus trivittatus* populations were present in the region at that time. It would be reasonable to suggest that clinal variation of AS/AL, LB/SB and PAL/PAW along the west coast of the United States (i.e., south of the area formerly occupied by the continental ice sheet) is similar to that existing during the Wisconsin glaciation. Probably the peak of mean values of AS/AL, LB/SB, and PAL/PAW in Washington or southwestern British Columbia represents the northern end of clinal variation of past populations. Subsequent retreat of the continental ice opened a coastal corridor and allowed contact between populations from the Alaskan-Yukon refugium and those immediately south of the ice sheet, thereby resulting in intermediate clinal values (Prince Rupert sample).

Chaoborus cooki. I studied seven samples, number 1–7 (Fig. 32), of fourth instar larvae of *Chaoborus cooki* in Alberta. Two additional samples from the Yukon, from along the Dempster Highway and from a pond on Klutlan Glacier moraine, were so similar to each other and distant from the Alberta samples, that I did not include them in this description.

A common geographical pattern is evident for four characters: head capsule length (Table 39), AS/AL (Table 40), number of mandibular fan bristles (Table 41), and number of anal fan setae (Table 42). Of the three samples from near Jasper, sample 3 is closest geographically to sample 5. Samples 2, 3,

and 4 are, although not in a straight line geographically, probably linearly arranged in terms of dispersal of this species along a continuous valley bordered, except to the eastward side of sample 3, by high mountains.

Table 28. Compound character index used to sex fourth instar larvae of *Chaoborus cooki* collected 32 km west of Edson, Alberta. Measurements in μm .

CHARACTER	INDEX VALUE									
	1	2	3	4	5	6	7	8	9	10
Antennal length	945- 970	971- 995	996- 1020	1021- 1045	1046- 1070	1071- 1095	1096- 1120	1121- 1145	1146- 1170	1171- 1195
Long antennal blade length	487- 499	500- 510	511- 522	523- 533	534- 545	546- 557	558- 568	569- 580	581- 591	592- 603
Postantennal filament length	649- 673	674- 696	697- 720	721- 743	744- 767	768- 791	792- 814	815- 838	839- 861	862- 885
Head capsule length	2030- 2074	2075- 2117	2118- 2161	2162- 2204	2205- 2248	2249- 2292	2293- 2335	2336- 2379	2380- 2422	2423- 2466

Table 29. Compound character index used to sex fourth instar larvae of *Chaoborus cooki* collected 1.6 km south of Jasper, Alberta. Measurements in μm .

CHARACTER	INDEX VALUE									
	1	2	3	4	5	6	7	8	9	10
Antennal length	870- 906	907- 943	944- 979	980- 1016	1017- 1052	1053- 1089	1090- 1125	1126- 1162	1163- 1198	1199- 1235
Long antennal blade length	539- 555	556- 572	573- 588	589- 604	605- 620	621- 637	638- 653	654- 669	670- 686	687- 702
Postantennal filament length	731- 748	749- 764	765- 781	782- 797	798- 814	815- 831	832- 847	848- 864	865- 880	881- 897
Head capsule length	1841- 1907	1908- 1973	1974- 2039	2040- 2105	2106- 2172	2173- 2238	2239- 2304	2305- 2370	2371- 2436	2437- 2502

Table 30. Variation in head capsule length (in μm) of fourth instar larvae of *Chaoborus trivittatus* in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	10	1888–2289	2083	236	99
2	11	1699–2207	1985	184	74
3	10	1546–1959	1785	198	83
4	11	1522–2065	1789	276	111
5	25	1487–2077	1702	215	57
6	11	1982–2266	2091	140	56
7	11	1794–2183	1985	200	81
8	12	1746–2199	1946	211	81
9	11	1687–2112	1885	202	82

Table 31. Variation in AS/AL of fourth instar larvae of *Chaoborus trivittatus* in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	0.86–0.92	0.901	0.026	0.012
2	11	0.85–0.92	0.888	0.031	0.012
3	10	0.86–0.91	0.884	0.024	0.010
4	11	0.84–0.91	0.878	0.031	0.012
5	26	0.82–0.92	0.878	0.041	0.011
6	10	0.86–0.92	0.901	0.026	0.011
7	11	0.88–0.92	0.905	0.021	0.008
8	12	0.86–0.92	0.894	0.032	0.012
9	11	0.86–0.91	0.887	0.030	0.012

Table 32. Variation in PAL/PAW of fourth instar larvae of *Chaoborus trivittatus* in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	10	4.50–7.00	5.263	1.094	0.461
2	11	4.29–5.50	4.983	0.470	0.189
3	10	4.54–5.42	5.002	0.472	0.199
4	11	4.33–6.62	5.288	0.874	0.351
5	26	3.79–6.77	5.442	0.830	0.217
6	11	4.15–6.18	5.075	1.010	0.406
7	11	4.54–7.33	5.847	1.184	0.476
8	12	4.75–9.14	5.656	1.875	0.722
9	11	4.54–7.30	5.558	1.267	0.509

Table 33. Variation in numbers of mandibular fan bristles of fourth instar larvae of *Chaoborus trivittatus* in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	10	23–29	25.9	2.9	1.2
2	11	16–23	20.0	3.4	1.4
3	10	17–23	19.7	3.7	1.6
4	11	14–21	17.4	3.6	1.4
5	26	12–24	17.2	4.7	1.2
6	11	18–24	21.4	2.7	1.1
7	11	19–25	22.2	3.0	1.2
8	12	18–30	23.0	5.3	2.0
9	11	18–26	22.5	3.2	1.3

Table 34. Variation in AS/AL of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	0.83–0.90	0.863	0.033	0.015
2	15	0.86–0.92	0.891	0.027	0.009
3	10	0.89–0.93	0.911	0.019	0.008
4	14	0.89–0.92	0.908	0.018	0.006
5	10	0.85–0.91	0.887	0.025	0.010
6	12	0.87–0.92	0.890	0.023	0.009
7	13	0.84–0.92	0.890	0.035	0.013

Table 35. Variation in LB/SB of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	8	1.76–2.18	2.040	0.200	0.094
2	15	1.80–2.49	2.110	0.280	0.097
3	10	2.39–2.81	2.510	0.222	0.094
4	14	2.12–2.92	2.530	0.272	0.097
5	10	1.95–2.44	2.240	0.249	0.105
6	12	1.47–2.34	2.040	0.334	0.129
7	12	1.85–2.37	2.080	0.236	0.091

Table 36. Variation in PAL/PAW of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	2.63–6.36	4.739	1.717	0.763
2	14	4.14–6.09	5.060	0.702	0.250
3	10	4.18–6.25	5.172	0.953	0.402
4	14	3.82–5.83	4.477	0.847	0.302
5	10	3.27–6.80	5.553	1.496	0.631
6	12	4.25–6.67	4.992	1.199	0.462
7	13	3.30–6.25	4.832	1.482	0.548

Table 37. Variation in numbers of mandibular fan bristles of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	11	18–33	27.7	6.6	2.6
2	15	21–36	26.2	6.1	2.1
3	10	22–29	24.7	4.2	1.8
4	14	20–32	25.5	4.2	1.5
5	10	20–29	24.0	3.9	1.7
6	12	21–30	23.8	3.7	1.4
7	16	18–31	22.3	5.8	1.9

Table 38. Variation in numbers of anal fan setae of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	31–33	32.0	1.3	0.6
2	15	27–31	28.6	2.0	0.7
3	10	26–38	27.4	1.0	0.4
4	14	26–29	27.9	1.3	0.5
5	10	25–29	27.0	1.9	0.8
6	12	27–30	28.4	1.4	0.5
7	12	25–30	27.1	2.1	0.8

Table 39. Variation in head capsule length (in μm) of fourth instar larvae of *Chaoborus cooki*. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	12	2148–2620	2396	204	79
2	10	1888–2360	2153	228	96
3	63	1841–2502	2153	217	37
4	17	1841–2325	2027	223	72
5	27	1770–2466	2178	260	67
6	13	2030–2443	2216	230	85
7	8	2065–2466	2304	236	111

Table 40. Variation in AS/AL of fourth instar larvae of *Chaoborus cooki*. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	12	0.81–0.89	0.856	0.038	0.014
2	11	0.81–0.89	0.850	0.035	0.014
3	62	0.80–0.89	0.851	0.031	0.005
4	17	0.81–0.87	0.832	0.023	0.007
5	27	0.80–0.90	0.854	0.038	0.010
6	13	0.80–0.93	0.866	0.046	0.017
7	8	0.83–0.88	0.864	0.025	0.012

Table 41. Variation in numbers of mandibular fan bristles of fourth instar larvae of *Chaoborus cooki*. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	14	13–21	15.4	2.9	1.0
2	11	11–14	12.9	1.4	0.6
3	62	11–15	13.5	1.5	0.3
4	17	12–17	13.9	2.0	0.7
5	27	10–15	12.9	1.6	0.4
6	13	12–16	13.8	1.6	0.6
7	8	13–17	14.5	2.1	1.0

Table 42. Variation in numbers of anal fan setae of fourth instar larvae of *Chaoborus cooki*. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	13	31–36	33.3	2.1	0.8
2	11	32–38	33.8	2.7	1.1
3	61	28–36	32.8	2.4	0.4
4	17	30–34	31.9	1.6	0.5
5	25	31–36	32.9	2.2	0.6
6	14	31–34	33.0	1.4	0.5
7	8	30–35	32.2	3.1	1.5

The pattern of geographical variation for the characters is similar. Sample 1 exhibits the highest average for all four characters with the exception of AS/AL. The three Jasper samples 2, 3 and 4, show a successive increase and decrease in mean value of number of mandibular fan bristles and number of anal fan setae, respectively. There is, generally, a successive increase of mean values of head capsule length, AS/AL, number of mandibular fan bristles and number of anal fan setae for samples 3, 5, 6 and 7. However, the following are exceptions to this pattern. Sample 5 mean number of mandibular fan bristles is less than that of sample 3. For AS/AL, the mean value of sample 6 is nearly identical to that of sample 7. For number of anal fan setae, the mean values of samples 5, 6 and 7 show no significant change.

Nevertheless, these overall patterns show that some of the greater differences among means may be attributable to this source. In addition, variation of number of anal fan setae of samples 2, 3 and 4 shows that characters vary significantly in a small geographic area and therefore, suggests either strong local selection or restricted gene flow between populations.

Compound character index and characters differing between fourth instar larvae of species of Schadonophasma. – Initially I had difficulty distinguishing between fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Although I could identify some populations using characters described by Saether (1970), I found variation of all individual characters to present a confusing continuum (see Fig. 21-25A) and was uncertain which characters could, in combination, be used to identify members of these two species. I therefore compared reared material of both sexes of *Chaoborus trivittatus* and *Chaoborus cooki*, used in analysis of sex-associated variation, to discover which characters might differ between the two species. Characters examined in the study of sex-associated variation differed significantly, except length of postantennal filaments (see Tables 25, 27) between male larvae and prelabral appendage width between female larvae. Identifications were confirmed through examination of associated adults.

For the purpose of this study I treated these two samples as if they were sympatric. Testing for species differences through initial comparison of samples collected from the same locality reduces differences due to geographic and ecotypic variation. However, such samples were not available to me when I initiated this study.

Six characters which differed between both males and females of *Chaoborus trivittatus* and

Chaoborus cooki and not correlated to each other, were chosen in order to construct a compound character index to give single values for individual specimens summarizing their features (Table 43). The correlation between LB/SB and AS/AL for *Chaoborus cooki* females and between PAL/PAW and number of mandibular fan bristles of male *Chaoborus cooki* were considered to be unimportant, especially as the correlation did not appear in the opposite sex of *Chaoborus cooki* or in either sex of *Chaoborus trivittatus*.

Range of each character was divided into 21 equal units numbered 0–20. The number 0 represented the extreme of *Chaoborus cooki* variation of a character and number 20 the opposite extreme of *Chaoborus trivittatus* variation. *Chaoborus cooki* larvae would therefore receive overall lower final index values than those of *Chaoborus trivittatus*. To compare all *Schadonophasma* species, the index, although based on differences between *Chaoborus trivittatus* and *Chaoborus cooki*, included the variation of *Chaoborus nyblaei*. Consequently the lowest index values of the number of mandibular fan bristles and two of the lowest values of number of anal fan setae, represent extremes of *Chaoborus nyblaei* variation.

The values of two specimens of *Chaoborus trivittatus* went beyond the recorded range of LB/SB and one each beyond the range of PAL/PAW and number of mandibular fan bristles. These specimens were given the highest index value for that character. It seems unlikely that these changes in procedure significantly affected the final results.

The distribution of index values for both *Chaoborus trivittatus* and *Chaoborus cooki* fourth instar larvae (Fig. 33) shows that almost all specimens can be identified with confidence. In addition, if more than seven specimens are examined, range of means of compound character values of *Chaoborus cooki* (34.0 – 43.3) and *Chaoborus trivittatus* (63.8 – 81.0) allows identification of all samples. Although one character was sex-associated for *Chaoborus cooki* and three for *Chaoborus trivittatus*, there was no significant difference between index values of male and female *Chaoborus trivittatus*. There was a significant difference between index values of male and female larvae of *Chaoborus cooki* but with a large degree of overlap. I therefore did not consider it important to separate male and female larvae. In addition, most samples were too small to confidently distinguish male and female larvae using a compound character index.

Chaoborus nyblaei fourth instar larvae (n=20) index values had a range of 16–47, mean of 36.4, 1.5SD of 11.6 and 2SE of 3.6. Therefore *Chaoborus nyblaei* fourth instar larvae can be distinguished from those of *Chaoborus trivittatus* but not from those of *Chaoborus cooki* using this index.

Specimens from Russell Lake, Alberta (n=10, range = 43–57, mean = 52.3, 1.5SD = 7.1, 2SE = 3.0), from Mechant Lake, Quebec (n=11, range = 50–62, mean = 57.1, 1.5SD = 6.8, 2SE = 2.7) and from Gallienne Lake, Quebec (n=19, range = 45–66, mean = 55.3, 1.5SD = 8.4, 2SE = 2.6) exhibited intermediate index values and could therefore not be identified. These samples are described and discussed below under 'Populations *incertae sedis*'.

Mean index values did not exhibit geographical patterns of variation. This was, probably, partially the result of independent patterns of geographical variation of individual characters evidenced, for example, by some characters of *Chaoborus trivittatus* larvae in Alberta.

On the basis of the above results I could determine that variation of each character for all samples studied, although with overlap, differed significantly between fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 21-25A; Table 6, 15). Fourth instar larvae of *Chaoborus nyblaei* were significantly different in all characters from those of *Chaoborus trivittatus* but were only significantly different from those of *Chaoborus cooki* in postantennal filament length, number of mandibular fan bristles and number of anal fan setae. Both second and third instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki* differed significantly for each character studied. First instars differed

Table 43. Compound character index used to recognize fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Measurement in μ m. (∞ = no data)

CHARACTER	INDEX VALUE																					
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Antennal length	1185-	1159-	1133-	1107-	1081-	1055-	1029-	1003-	997-	951-	925-	899-	873-	847-	821-	795-	796-	743-	717-	691-	655-	
	1210	1184	1158	1132	1106	1080	1054	1028	1002	976	950	924	898	872	846	820	794	768	742	716	690	
LB/SB	1.08-	1.16-	1.24-	1.32-	1.40-	1.48-	1.56-	1.64-	1.72-	1.80-	1.88-	1.96-	2.04-	2.12-	2.20-	2.28-	2.36-	2.44-	2.52-	2.60-	2.68-	
	1.15	1.23	1.31	1.39	1.47	1.55	1.63	1.71	1.79	1.87	1.95	2.03	2.11	2.19	2.27	2.35	2.43	2.51	2.59	2.67	2.75	
AS/AL	.75	.76	.77	.78	.79	-	.80	.81	.82	.83	.84	.85	.86	.87	.88	-	.89	.90	.91	.92	.93	
PAL/PAW	1.70-	2.06-	2.42-	2.78-	3.14-	3.50-	3.86-	4.22-	4.58-	4.94-	5.30-	5.66-	6.02-	6.38-	6.74-	7.10-	7.46-	7.82-	8.18-	8.54-	8.90-	
	2.05	2.41	2.77	3.13	3.49	3.85	4.21	4.57	4.93	5.29	5.65	6.01	6.37	6.73	7.09	7.45	7.81	8.17	8.53	8.89	9.25	
No. mandibular fan bristles	8,9	10	11	12	13,14	15	16	17	18,19	20	21	22	23,24	25	26	27	28,29	30	31	32	33,34	
No. anal fan setae	40	39	38	37	36	-	35	34	33	32	31	30	29	28	27	-	26	25	24	23	22	

in all characters except LB/AL and postantennal filament length.

Saether (1970: 21) recognized number of mandibular fan bristles (23-32), LB/SB (1.8 – 2.3) and LB/AL (0.70 – 0.79) as diagnostic for *Chaoborus brunskilli* fourth instar larvae. However, it is clear from the distribution of these characters of larvae of *Chaoborus trivittatus* (Fig. 34A-C) that these characters do not exhibit any bimodality suggestive of another species, and cannot be used to distinguish the larvae placed in *Chaoborus brunskilli* as members of a separate taxon.

Because some species of *Chaoborus* exhibit a limited range of number of mandibular fan bristles Saether (1970: 18) argued that 'At least it seems very unlikely that a variation of 11-32 setae, the total variation within *Schadonophasma* (*sic*), may be accounted for by the presence of only one or two species'. I can see no justification for such an argument. Determination of a large range of variation of a character, such as the number of mandibular fan bristles of *Chaoborus trivittatus* reported here, is not a valid criterion for suspecting the presence of more than one species.

Variation of characters of pupae

Pupal material was identified on the basis of reared material, of association with known larvae, of geographical distribution of the species or, observations of pharate adult characters.

The most detailed, recent description of pupae of all species of *Schadonophasma* has been provided by Saether (1970). All material was correctly identified with the exception of pupae of *Chaoborus brunskilli* (= *Chaoborus trivittatus*). The pupa from Stanford, California was not reexamined but the locality from which it was collected and its association with larvae of *Chaoborus trivittatus* shows clearly that this specimen was correctly identified.

Saether (1970), however, did not take into account the marked sex-association variation. His description of *Chaoborus cooki* pupae included four males, of *Chaoborus brunskilli* (= *Chaoborus trivittatus*) one male, and of *Chaoborus nyblaei* two males and ten females. The sex of the pupa of *Chaoborus trivittatus* is not known, but as Saether (1970) recorded genital sac length only for male pupae, and did not do so for this specimen, suggests that it was a female.

Descriptive statistics for both sexes of each species for most characters described below are given in the species descriptions and comparison of that data shows only those characters presented in the keys to be useful for species determination.

Because of the small size of individual samples, to estimate sex associated variation of *Chaoborus trivittatus* and *Chaoborus cooki* pupae I compared all males with all females within each species. Compared material of *Chaoborus nyblaei* was from a single locality. Seven characters were studied: abdomen length; length, width and length/width of respiratory horns; and length, width and width/length of abdominal segment seven. The shape and size of the genital lobes differs markedly between male and female *Chaoborus* pupae (Fig. 2C,D; Deonier, 1943: fig. 1,2). In addition, female pupae are slightly darker in overall coloration than males collected from a single locality.

Five characters were sex associated in pupae of *Chaoborus trivittatus*: length and width of respiratory horns; length and width of abdominal segment seven; and total abdominal length. Length, width and length/width of the respiratory horns; and length and width of abdominal segment seven were sex associated for pupae of *Chaoborus cooki*; for pupae of *Chaoborus nyblaei* length and width of respiratory horns; length, width and width/length of abdominal segment seven; and total abdominal length were sex-associated.

It is reasonable to assume that length and width measurements are sex-associated because of a difference in overall size of male and female pupae. Total abdominal length is sex-associated in pupae of *Chaoborus trivittatus* but not in those of *Chaoborus cooki*. This probably reflects stage of development of eggs, which may distend the abdomen and are more developed in older female pupae of *Chaoborus*

trivittatus than in *Chaoborus cooki*. Because this character is sex-associated for pupae of *Chaoborus nyblaei* this suggests that ovaries of this species develop in a similar fashion to *Chaoborus trivittatus*.

Saether (1970: 18) noted that width/length of abdominal segment VII (erroneously stated as VIII) is 1.4 for *Chaoborus trivittatus*, 1.5 for *Chaoborus brunskilli* (= *Chaoborus trivittatus*), 1.6 for *Chaoborus cooki*, and 1.7–1.9 for *Chaoborus nyblaei* pupae. Examination of Tables 4, 5, 13, 14, 20 and 21 shows extensive overlap of range of this character between males or females of each species.

Coloration differences noted by Saether (1970) were unreliable when more material was examined. There is little doubt that ethanol preserved specimens lose at least some of their color with time. In addition, Saether (1967) has shown that coloration of the anal paddle ribs varies extensively within pupae of *Chaoborus flavicans*. However, his results may be biased through use of specimens treated with KOH.

Differences of the angle of the abdomen in relation to the longitudinal axis of the body between pupae of *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 5A,B) were observed from most of the samples as they were collected and/or reared in the laboratory, from localities in Alberta during the course of this study. The character was consistent for identification of pupae examined.

Differences in pupal ovarian development of *Chaoborus trivittatus* and *Chaoborus cooki* were apparent (see key to female pupae) and this trait is also expressed in the stage of ovarian development in teneral female adults (see below). In live female pupae of *Chaoborus trivittatus* at least 48 hours old (at 20 C) ovaries are macroscopically apparent as white elongate organs in the abdomen (see Parma, 1971b: 40). These are not apparent in female pupae of *Chaoborus cooki*.

Variation of characters of male adults

Saether (1970) noted two characters of diagnostic value for determination of adult males to species: shape of penis valves and X/Y wing ratio. These two characters were studied in detail. Other differences between males of the three species of *Schadonophasma* are available by comparison of the descriptions (Table 2, 11). Characters differing significantly between male adults of *Chaoborus trivittatus* and *Chaoborus cooki* are Rsa length, all leg measurements, gonocoxite and gonostylus length, Y/X, number of tergite IX setae and penis valve length.

Differences in coloration of adults of *Chaoborus trivittatus* and *Chaoborus cooki* (see descriptions) may in part be ecophenotypic. Bradshaw (1973: 1256) mentions that male adult *Chaoborus americanus* are a darker color when reared at temperatures below 15 C, and this may also have an effect on color variation of adult *Schadonophasma* (also see Rapoport, 1969; Vernberg, 1962).

Range of variation of Y/X of male adults of *Chaoborus trivittatus* (Table 2) and *Chaoborus cooki* (Table 11), although significantly different, exhibits extensive overlap. Range of variation of Y/X of *Chaoborus nyblaei* male adults (see description) is within the range of Y/X of both *Chaoborus trivittatus* and *Chaoborus cooki*.

I studied geographical variation of this character for *Chaoborus trivittatus* and *Chaoborus cooki* but, possibly because of the small number of samples, recognized no patterns. However, it is clear that the ratio, at least for *Chaoborus trivittatus*, varies markedly in a relatively small geographical area. A sample from 16 km west of Jasper, Alberta, ($n=38$, range = 1.35–2.18, mean = 1.705, 1.SSD = 0.310, 2SE = 0.067) differed significantly from a sample from 2.4 km west of Edmonton, Alberta, ($n=40$, range = 1.54–2.42, mean = 1.915, 1.SSD = 0.309, 2SE = 0.065).

Saether (1970) distinguished four types of penis valves characteristic of each of the four species he described. Apparently because of the similarity of penis valves of the male from Baffin Island with those of the specimen from Finland, he identified the former specimen as *Chaoborus nyblaei*. In addition, differences in the penis valves of the male from Lk. 241, Kenora, Ontario supported his recognition of

the larvae from that area as indicative of the new species of *Chaoborus brunskilli*. However, these penis valves were not examined in a standard orientation. Reorientation of the penis valves of the specimens from Baffin Island and Lk. 241, Kenora resulted in forms indistinguishable from those typical of *Chaoborus trivittatus*. The dark, very short tips of the penis valves of *Chaoborus nyblaei*, as drawn by Saether (1970: fig. 7A,B), are actually the claws pointing downward. Outlines of a single penis valve of a male *Chaoborus trivittatus* (Fig. 12A-E), drawn from different aspects, shows that one orientation (Fig. 12D) is very similar to that thought by Saether (1970: fig. 7A,B) to be typical of *Chaoborus nyblaei*, and another (Fig. 12B) typical of *Chaoborus brunskilli* (Saether, 1970: fig. 7C). The effect of changed orientations of a single penis valve of *Chaoborus cooki* (Fig. 12F-J) shows the importance of examining the penis valves from different aspects. For example, one orientation of the valve of a male of *Chaoborus cooki* (Fig. 12F), is extremely similar to one orientation of the penis valve of *Chaoborus trivittatus* (Fig. 12A). For the purposes of this study only Figures 12E and 12H show useful orientations. Of the material I examined, no penis valves of *Chaoborus trivittatus* looked like those of *Chaoborus cooki* when in this orientation.

The two types of penis valves recognized by Saether (1970: 27) to be typical of two forms of *Chaoborus americanus* are also a result of examination of material from different aspects (pers. obs.).

Because of the seemingly impossible prospects of completely standard orientation of penis valves, even though all specimens were drawn with the penis valve head in a horizontal plane, it is not known to what degree this affected the drawings of intraspecific and interspecific variation of penis valves of *Chaoborus trivittatus* (Fig. 10A-O) and *Chaoborus cooki* (Fig. 11A-N). Although a comparison between amount of intrapopulational and interpopulational variation of penis valves of either *Chaoborus trivittatus* or *Chaoborus cooki* do not show very marked differences in these figures, there is actually more interpopulational than intrapopulational variation.

The penis valves of male *Chaoborus nyblaei* are illustrated in Fig. 11 O,P.

Length of penis valves differed significantly between *Chaoborus trivittatus* and *Chaoborus cooki*, even though the entire range of variation of that of *Chaoborus cooki* was contained in the range of variation of length of penis valves of *Chaoborus trivittatus*. Length of penis valves of *Chaoborus nyblaei* was within the range of both *Chaoborus cooki* and *Chaoborus trivittatus*.

The only apparent pattern of geographical variation of the length of penis valves was found in specimens of *Chaoborus trivittatus* from along the west coast of North America (Table 44). Although this linear increase in mean values cannot be confidently interpreted on its own, geographical variation in five larval characters in this region suggests that the pattern is significant (see section on geographical variation of fourth instar larvae).

Number of setae on one side of tergite IX was studied only because it was convenient to do so when examining penis valves. Saether (1970) has already shown a large amount of overlap of variation of this character between *Chaoborus trivittatus* and *Chaoborus cooki*, although analysis here does indicate them to be significantly different. I could detect no patterns of geographical variation of this character for either species.

Variation of characters of female adults

The only diagnostic feature of females given by Saether (1970) was Y/X wing ratio of *Chaoborus trivittatus* and *Chaoborus cooki*. Female adults were not available for *Chaoborus nyblaei*.

I identified females on the basis of their temporal and geographical association with males, geographical distribution or type of ovarian development and egg type. I studied only variation of Y/X wing ratio in detail. Other differences between females of these species are in the descriptions.

Table 44. Variation of penis valve length (in μm) of male adult *Chaoborus trivittatus*.

Sample 1 from Pacific Grove, Stanford, Oakland and Mad River Beach, California. Sample 2 from Hoodspoint, Port Madison and Bremerton, Washington, and Kaslo, British Columbia. Sample 3 from Prince Rupert and Terrace, British Columbia.

Sample	N	Range	Mean	1.5SD	2SE
1	9	145–191	167.6	20.6	9.2
2	14	162–209	180.6	17.7	6.3
3	8	168–197	190.0	14.5	6.8

Characters which differed significantly between *Chaoborus trivittatus* and *Chaoborus cooki* were length of penultimate antennal article, prementum length, HW/Pl, number of anepisternal setae, all leg measurements, and seminal capsule diameter. Number of setae on the comb of the third tarsomere of either midleg or hindleg has not been previously recorded but was found to differ significantly between the two species.

Although means of the ratio Y/X of female adult *Chaoborus trivittatus* and *Chaoborus cooki* differ significantly, ranges overlap extensive (Table 3, 12). Mean values did not exhibit geographical patterns of variation. As with males, this character of females can vary markedly in a relatively short distance. A sample from 16 km west of Jasper, Alberta, ($n=10$, range = 2.03–2.86, mean = 2.414, 1.5SD = 0.425, 2SE = 0.179) differed significantly from a sample 2.4 km west of Edmonton, Alberta, ($n=28$, range = 1.57–3.22, mean = 2.267, 1.5SD = 0.538, 2SE = 0.136). However, a sample from eight localities in California ($n=19$, range = 1.19–2.95, mean = 1.919, 1.5SD = 0.653, 2SE = 0.200) did not differ significantly from a sample from Terrace and Atlin, British Columbia and Whitehorse, Yukon, ($n=15$, range = 1.46–2.56, mean = 2.011, 1.5SD = 0.444, 2SE = 0.153).

Females of *Chaoborus trivittatus* and *Chaoborus cooki* differ in ovarian development. Female *Chaoborus trivittatus* less than one hour old, reared from fourth instar larvae collected 2.4 km west of Edmonton, Alberta, had abdomens full of eggs. Ovaries of some females extended into the thorax. A ratio of distance of the anterior tip of the longest ovary from the end of the abdomen/abdominal length was 0.71–1.11 (mean = 0.967). The ovaries together contained 251–329 (mean = 279) eggs which, at this stage, were each at least 348 μm long. Fedorenko (1975c: 3102) recorded 161 ± 7.4 SE eggs per female pupae from Eunice Lake, British Columbia.

Females of *Chaoborus cooki* less than 12 hours old, collected as early instars 1.6 km south of Jasper, or as fourth instar larvae, 1.4 km west of George Lake, Alberta, had much smaller ovaries with a ratio of the distance of the anterior tip of the longest ovary from the tip of the abdomen/abdominal length of 0.32–0.62 (mean = 0.444). Total number of eggs present was 74–95 (mean = 86). Each egg in a teneral female is no more than 120 μm long. Teneral females of these two species can therefore be distinguished from one another by size of ovaries. A nulliparous female can be identified by number of eggs present. If an individual with at least some eggs present is suspected of being parous, the eggs are developed enough to distinguish the type. A thick exochorion is typical of *Chaoborus cooki* (Fig. 9C) and a thin exochorion of *Chaoborus trivittatus* eggs (Fig. 9A).

I had available only two females of *Chaoborus nyblaei* which still had eggs in their abdomens. One was the lectotype and its abdomen contained eggs with a thick exochorion (Fig. 9B). I could not count the number of eggs present. The other female, from Abisko, Sweden, had the same type of egg and its abdomen contained 58 eggs. Implications of differences in egg type are discussed below in the section on development of eggs.

Descriptions of populations *incertae sedis*

Three samples of larvae and one of pupae could not be identified with certainty. The three larval samples exhibited compound character index values (see p. 174) intermediate between those of *Chaoborus trivittatus* and *Chaoborus cooki*. Although the two samples from Mechant and Gallienne Lakes, Quebec are here described separately, they possibly belong to the same reproductive population, considering the close proximity of the lakes. Pope *et al.* (1973) recognized samples from these two lakes as members of a new species or subspecies of *Schadonophasma* but did not describe them.

Several interpretations of these samples seem equally reasonable. Individuals may belong to one or more new species or they may be hybrids between *Chaoborus trivittatus* and *Chaoborus cooki*, although number of specimens would seem too large to be the product of hybridization (see section on mating experiments). Also, specimens may be members of *Chaoborus cooki*. Data from the sample from Russell Lake, Alberta, shape of prelabral appendages of all larvae of all samples, and shape of penis valves of pupae from Gallienne Lake, Quebec, suggests the likelihood of this (see below for details). None of the specimens in the analysis of *Chaoborus cooki* came from lakes. *Chaoborus cooki* may possibly invade this habitat and resultant individuals may therefore be phenotypically different from individuals of *Chaoborus cooki* described in this study. Sikorowa (1973) has shown that habitat influences variation of characters of larvae of *Chaoborus flavicans*. Examination of adults, study of geographical variation once more material is available, especially from eastern Canada, study of the life cycle, and developmental studies could be used to test this possibility.

Sample from Russell Lake, Alberta. – All specimens collected (I-VIII-1969) were fourth instar larvae. The population from which this sample was taken is within the geographical range of both *Chaoborus trivittatus* and *Chaoborus cooki*. Coloration is as other members of the subgenus. Measurements and proportions are given in Table 45.

Table 45. Descriptive statistics for fourth instar larvae of *Schadonophasma* from Russell Lake, Alberta. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	13	1884–2060	1975	94	35
Antennal length	12	835–947	913	52	20
LB/SB	10	1.71–2.12	1.91	0.18	0.07
LB/AL	12	0.74–0.91	0.800	0.075	0.029
AS/AL	12	0.79–0.90	0.847	0.053	0.020
Postantennal filament length	13	761–882	829	55	21
PAL/PAW	13	1.76–2.44	2.09	0.29	0.11
Number mandibular fan bristles	13	15–19	17.5	1.8	0.7
Number anal fan setae	13	27–30	28.9	1.6	0.6

Variation of most characters gave no clues as to whether this sample might be composed of larvae of either *Chaoborus trivittatus* or *Chaoborus cooki*, or of a third undescribed species, because the range of these characters was within the range of variation of both *Chaoborus trivittatus* and *Chaoborus cooki*. Low PAL/PAW values would suggest the sample is conspecific with *Chaoborus cooki*. However, some specimens exhibit LB/AL values, number of mandibular fan bristles, and number of anal fan setae which are beyond the range of *Chaoborus cooki* and into the range of variation of *Chaoborus trivittatus*.

All characters were examined in relation to clinal variation of these characters of both *Chaoborus trivittatus* and *Chaoborus cooki* for clues of conspecificity. Only mean number of mandibular fan bristles may possibly be explained by clinal variation of this character of *Chaoborus cooki* fourth instar larvae.

All material deposited with ABO_r.

Sample from Mechant Lake, Quebec. – All specimens were collected (14-VII-1975) as fourth instar larvae. Although Pope *et al.* (1973) report that a population represented by this sample coexisted with larvae of *Chaoborus trivittatus*, I did not examine any material of *Chaoborus trivittatus* which would have given better clues concerning possibilities of the two being conspecific. However the recognition of two forms in a single lake does not negate possibilities of them being conspecific. Fedorenko and Swift (1972) described two forms of *Chaoborus trivittatus* which differed in size and color but merely represented two overlapping generations.

Larvae are darker than any other *Chaoborus* larvae I have examined. Head capsules were notably darker. In particular, dorsum of head capsule, area around the anterior tentorial pits and dorsal from each pit to dorsum of head capsule, posterior edge of head capsule including ocular-antennal segment, ventral edge of head capsule between antennae and labrum, antennae, maxillary palpus and seta, and anal fan setae were all more darkly pigmented. All thoracic and abdominal segments were infuscated dorsally. Measurements and proportions are given in Table 46.

Some individuals have AS/AL and PAL/PAW values within the range of *Chaoborus cooki* and beyond the range of *Chaoborus trivittatus*. Conversely, some individuals exhibited head capsule length, antennal length, LB/SB, LB/AL, and number of mandibular fan bristles within the range of variation of those characters of *Chaoborus trivittatus* and beyond the range of those of *Chaoborus cooki*.

All material deposited with ABO_r.

Sample from Gallienne Lake, Quebec. – All specimens were collected (13-VIII-1971) as fourth instar larvae. Color of larvae was similar to that of larvae from Mechant Lake, Quebec. For measurements and proportions see Table 47.

Some individuals exhibited LB/SB, LB/AL ratios and number of anal fan setae beyond the range of variation of these characters for *Chaoborus cooki* but within the range of those of *Chaoborus trivittatus*. Prelabral appendages were typical of those of *Chaoborus cooki* larvae. Head capsule, antennal and postantennal filament length, and number of mandibular fan bristles of this sample differed significantly from those of larvae from Mechant Lake. However, this might be explained by geographical variation or differences in habitat. No ratios significantly differed between the two samples.

Pupae were darker than any other *Chaoborus* material examined. Measurements and proportions of male pupae are given in Table 48, and of female pupae in Table 49. Nearly all measurements of both male and female pupae were within, or less than, the range of variation of *Chaoborus trivittatus*. Only the WS/LS of male pupae was within the range of WS/LS of both *Chaoborus trivittatus* and *Chaoborus cooki*.

Penis valves were developed in three male pupae but, because these could not be removed to study from different orientations without destroying the rest of the specimen, they were difficult to interpret. Penis valves of one of these individuals were most similar to those of *Chaoborus cooki* adults. However, length of penis valves ranged from 156.6–162.4 μm . Because material had been previously cleared I could not determine the degree of ovarian development of two parate female adults. One specimen had well developed seminal capsules with a diameter of 50.0 μm .

All material deposited with OASa.

Table 46. Descriptive statistics for fourth instar larvae of *Schadonophasma* from Mechant Lake, Quebec. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	11	1617–1782	1682	71	29
Antennal length	11	731–777	757	24	10
LB/SB	11	1.71–2.15	1.99	0.13	0.05
LB/AL	11	0.79–0.91	0.843	0.046	0.019
AS/AL	11	0.77–0.89	0.841	0.054	0.022
Postantennal filament length	11	637–708	687	31	12
PAL/PAW	11	2.50–3.08	2.82	0.28	0.11
Number mandibular fan bristles	11	12–15	13.2	1.5	0.6
Number anal fan setae	11	26–29	27.5	1.6	0.6

Table 47. Descriptive statistics for fourth instar larvae of *Schadonophasma* from Gallienne Lake, Quebec. Measurements in μm .

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	19	1876–2183	2029	142	42
Antennal length	19	824–974	908	66	20
LB/SB	19	1.85–2.27	2.08	0.21	0.06
LB/AL	19	0.75–0.86	0.810	0.052	0.016
AS/AL	19	0.75–0.91	0.843	0.059	0.018
Postantennal filament length	19	743–861	809	51	12
PAL/PAW	19	1.71–4.00	2.67	0.68	0.21
Number mandibular fan bristles	20	13–17	15.4	1.5	0.4
Number anal fan setae	20	25–29	27.2	1.9	0.6

Table 48. Descriptive statistics for male pupae of *Schadonophasma* from Gallienne Lake, Quebec. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdominal length (mm)	4	5.5–5.9	5.72	–	–
Respiratory horn length (mm)	4	1.06–1.23	1.112	–	–
Respiratory horn width (mm)	4	0.30–0.32	0.307	–	–
Abdominal segment VII length	9	767–885	821	62	28
Abdominal segment VII width	4	1133–1263	1192	–	–
WS/LS	4	1.45–1.49	1.48	–	–

Table 49. Descriptive statistics for female pupae of *Schadonophasma* from Gallienne Lake, Quebec. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdominal length (mm)	8	4.3–5.6	4.81	0.61	0.29
Respiratory horn length (mm)	3	1.07–1.17	1.117	–	–
Respiratory horn width (mm)	4	0.27–0.31	0.289	–	–
Abdominal segment VII length	9	814–885	852	40	18
Abdominal segment VII width	8	979–1227	1136	116	55
WS/LS	8	1.20–1.42	1.32	0.098	0.046

BIONOMICS

Studies of life histories, developmental characteristics, and behavior give important information on questions of conspecificity, and suggest how species closely related retain their reproductive unity, such studies are also important in interpretation of characters used to infer the evolutionary history of such species and the events pertaining thereto. In this section I present observations made on *Chaoborus trivittatus* and *Chaoborus cooki* in Alberta. These are used to infer some probable bionomic features of *Chaoborus nyblaei* in Fennoscandia. For the following analysis observations were made of events which I had the opportunity and time to deal with and which I believed to be most informative to elucidate species differences and their evolution. A more complete, general account of such bionomic information has been presented by Parma (1971b).

Life cycle

All temperate *Chaoborus* species previously studied exhibit a life cycle in which fourth instar larvae overwinter, pupate in spring, emerge as adults which lay eggs and develop to fourth instar larvae by winter (Balvay, 1977d; Bradshaw, 1973; Fedorenko and Swift, 1972; Parma, 1971b; Sikorowa, 1973). In multivoltine populations these fourth instar larvae result in another adult emergence and subsequent larvae but, regardless of number of generations per year, every temperate species studied overwinters as fourth instar larvae. For this reason, immatures of these species are usually present only in permanent waters. Studies of tropical species (Corbet, 1958; Lewis, 1975; MacDonald, 1956; McGowan, 1974, 1975; Tjønneland, 1958; Verbeke, 1957) suggest that these are also restricted to permanent waters. Records of *Chaoborus* larvae in temporary waters in the tropics (Belkin and Heinemann, 1975, 1976; Heinemann and Belkin, 1977a, 1977b; Panday, 1975) can be explained as incidental as McGowan (1974: 498) observed adult females of *Chaoborus anomalus* and *Chaoborus ceratopogones* (Theobald), species restricted to permanent waters in Africa, laying eggs in dishes of water in which the larvae undoubtedly would not survive.

Records of larvae of temperate *Chaoborus* species from temporary waters (e.g. Anderson and Raasveldt, 1974: 16) are likely from either a single generation of a multivoltine population which overwintered elsewhere in permanent waters, a population which eventually became extinct (see p. 186), or are larvae which were transferred from over-flowing ponds upstream on a river to downstream inundation pools. Merely the presence of *Chaoborus* larvae in an aquatic habitat is not sufficient evidence to suppose survival of the population in this habitat. Records of *Chaoborus americanus* and *Chaoborus flavicans* fourth instar larvae from the Red Deer river, near Innisfail, Alberta, when the river still had ice on its edge, showed all specimens with empty guts, suggestive of their inability to successfully survive to adulthood in this habitat. These larvae probably were washed into this permanent river from ponds further upstream. Records of *Chaoborus* larvae from the Hudson River, New York (Beck *et al.*, 1975) are undoubtedly larvae from impoundments further upstream. Peus's (1934) often cited record of *Chaoborus flavicans* from inundation pools along rivers in Germany and Reisen's (1973) observation of a single specimen of *Chaoborus punctipennis* from an inundation pool near a river in Oklahoma are therefore probably from larvae washed downstream from flooded ponds. Retreat of an over-flowing river in inundation areas can leave intact a population of *Chaoborus* larvae (Heinemann and Belkin, 1977a: 272, Roback, 1966; see p. 185).

Chaoborus trivittatus. Fedorenko and Swift (1972) found a population of *Chaoborus trivittatus* in an oligotrophic lake in southwestern British Columbia to be composed of two overlapping generations. Fourth instar larvae overwintered for two consecutive winters before pupating. Although adults emerged every spring, larvae which had overwintered only one winter did not pupate. Continual presence of

fourth instar larvae throughout and after the pupal emergence period is therefore indicative of this two year life cycle.

I studied the life cycle of *Chaoborus trivittatus* in a pond 2.4 km west of Edmonton which measured approximately 18 by 85 meters, had a maximum depth of about two to three meters, and was densely shaded by mature stands of *Populus balsamifera* and *Picea mariana*. Sampling during 1975 (Table 50) produced a few fourth instar larvae on May 13, all of which pupated by May 26. These data indicate a univoltine population of *Chaoborus trivittatus*. Changes in pupal and pupal exuvial sex ratios is explained by earlier pupation of male larvae (Table 51) and less time for development of male pupae (p. 193). Emergence of adults was restricted to later in May. Eggs hatched in three to four days under laboratory conditions.

Table 50. Number of *Chaoborus trivittatus* immatures collected 2.4 km west of Edmonton, Alberta.

DATE	LARVAL INSTARS				PUPAE		PUPAL EXUVIAE	
	1	2	3	4	Male	Female	Male	Female
26-IV-1975	-	-	-	234	-	-	-	-
8-V-1975	-	-	-	5	218	156	-	-
13-V-1975	-	-	-	2	186	274	195	134
26-V-1975	106	11	40	-	-	3	-	1
12-VI-1975	25	22	144	-	-	-	-	-
13-VIII-1975	-	-	-	72	-	-	-	-

Table 51. Numbers of pupae resulting from 45 individually reared fourth instar larvae of *Chaoborus trivittatus* collected 2.4 km west of Edmonton, Alberta, 25-IV-1975.

Date	Male	Female
28-IV	18	4
29-IV	5	14
30-IV	-	3
4-V	-	1
Total:	23	22

Overwintering of fourth instar larvae as a feature of *Chaoborus trivittatus* is reflected in the range of collection dates of material examined (Fig. 25B). Gaps in the record undoubtedly reflect lack of collected material (Fedorenko and Swift, 1972; Main, 1953). James and Smith (1958) also observed overwintering of some *Chaoborus trivittatus* larvae (as *Chaoborus nyblaei*).

Parma (1971b) has discussed how univoltine or multivoltine *Chaoborus* populations are a result of environmental factors and vary in response to type of habitat and geographical area. These observations explain the differences between the bivoltine life cycle of *Chaoborus trivittatus* described by Fedorenko and Swift (1972) and the univoltine life cycle described here. In addition, temporal bimodality of records of field collected adults in southern Ontario and Quebec and northeastern United States (Table 52) suggest that some populations of the species are multivoltine in this region (see Balvay, 1977c; Hirvenoja, 1960, 1965; Parma, 1971b).

Table 52. Records of field collected adult *Chaoborus trivittatus* from southern Ontario and Quebec and northeastern United States. Roman numerals represent months and Arabic numerals are: 1=Days 1–10, 2=Days 11–20; 3=Days 21–30(31).

	1-IV	2-IV	3-IV	1-V	2-V	3-V	1-VI	2-VI	3-VI	1-VII	2-VII	3-VII	1-VIII	2-VIII	3-VIII	1-IX	2-IX	3-IX
North Burgess Twp., Ontario				x														
Black Lake., Ontario			x															
Cordova Mines, Ontario																	x	
Lac de Jean Venne, P.Q.		x		x	x													
Old Chelsea, P.Q.																	x	
Worcester, Massachusetts			x															
Hampton, New Hampshire			x					x										
Elizabethtown, New York							x	x						x				
Bear Mountain, New York																		x

Chaoborus cooki. The only previous allusion to the life cycle of *Chaoborus cooki* has been by James and Smith (1958) who mention that some of the populations of *Chaoborus nyblaei* (probably = *Chaoborus trivittatus* and *Chaoborus cooki*) at Churchill, Manitoba, overwintered as eggs.

The life cycle of *Chaoborus cooki* was studied at three locations. A pond 1.6 km south of Jasper measured 10 by 41 meters with a maximum depth of 0.9 m during most of its existence. Shading on the north, south and west sides of the pond was provided by *Salix* sp. and *Picea mariana*. The pond was located about 40 m from the south bank of the Miette River and, although it did not initially receive its water from the river, I observed overflow of its banks and flooding of the pond to about six times its normal surface area on two occasions, on 19-VI-1976 and 30-VI-1976. Retreat of the river from this inundation zone seemed to leave most of the population of *Chaoborus cooki* intact. However, I did collect several larvae stranded in isolated pools which drained within one day after retreat of the river. This pond was dry by October 8, 1976.

A pond 32 km west of Edson measured 11 by 29 meters, with a maximum depth of 0.7 m during most of its existence and was well shaded by dense brush and trees of *Picea mariana* and *Populus tremuloides*. The pond was dry by October 8, 1976.

A third pond, 1.4 km west of George Lake, measured 15 by 19 meters and had a maximum depth of 0.9 m during most of its existence. Although surrounded by dense brush and trees of *Picea mariana* and *Populus tremuloides* on its north, east and west sides the pond was often in direct sunlight. However, larvae were almost always located in the shade of numerous *Typha* sp. The pond dried up on two occasions, 23-VII-1976 and 30-X-1976.

Tables 53, 54 and 55 give numbers of animals collected from these three sites. A common type of life cycle is apparent. There is a progression within one growing season, of first through fourth larval instars, pupation, and, observed at 1.4 km west of George Lake and 1.6 km south of Jasper, emergence of adults. Lack of records of larvae after the pupal period until the next spring suggests that *Chaoborus cooki* overwinters in these temporary aquatic habitats as eggs. This conclusion is supported by observed diapause of *Chaoborus cooki* eggs in the laboratory and their resistance to desiccation (p. 191). However, in spite of this adaptation to temporary waters, *Chaoborus cooki* larvae may occasionally live in permanent ponds (e.g. 2.4 km west of Edmonton).

This univoltine life cycle, in which the eggs overwinter, is reflected in the restricted temporal distribution of records of fourth instar larvae of *Chaoborus cooki* (Fig. 25B).

It is clear that this species circumvents the problems presented by temporary habitats to other *Chaoborus* species. Larvae of *Chaoborus americanus* were collected late in the season from each of the three sites studied (Tables 53, 54, 55) and those remaining undoubtedly died when the ponds became dry. Both live and dead *Chaoborus trivittatus* larvae and a live *Chaoborus americanus* fourth instar larva were taken off wet mud at the location 1.4 km west of George Lake on 18-IX-1976.

The unique life cycle of *Chaoborus cooki* in temporary ponds allows this species to avoid competition with other sympatric *Chaoborus* species, except when some of these occasionally inhabit the same temporary ponds. Even so, these would be as younger instars than those of *Chaoborus cooki*.

Chaoborus nyblaei. There is no direct evidence of the type of life cycle of *Chaoborus nyblaei*. However, a thick exochorion, similar to that of *Chaoborus cooki* would suggest that the egg is similarly adapted to resist desiccation and that this species also overwinters as eggs. *Chaoborus nyblaei* larvae have been collected from both a large permanent pond, and a small pool a few meters in diameter, in northern Fennoscandia (Hirvenoja, 1961).

Low number of eggs per female would support the conclusion that *Chaoborus nyblaei* immatures inhabit temporary ponds. Collection of adults only in the later part of July agrees with this interpretation of the type of life cycle.

Table 53. Numbers of *Chaoborus cooki* immatures collected 1.6 km south of Jasper, Alberta.
symbolizes dry conditions.

DATE	LARVAL INSTARS				PUPAE		PUPAL EXUVIAE	
	1	2	3	4	Male	Female	Male	Female
20-V-1975	—	3	27	—	—	—	—	—
4-VI-1975	—	—	2	34	—	—	—	—
17-VI-1975	—	—	1	33	20	1	—	—
*13-VII -1975	—	—	—	—	—	—	—	1
25-IV-1976	93	7	—	—	—	—	—	—
18-V-1976	—	10	48	—	—	—	—	—
31-V-1976	—	—	53	20	—	—	—	—
13-VI-1976	—	—	2	18	—	—	—	—
30-VI-1976	—	—	—	14	5	—	—	—
*9-IX-1976	—	—	—	—	—	—	—	—
8-X-1976	#####							
28-IV-1977	91	32	—	—	—	—	—	—
12-VII-1977	—	—	—	31	7	3	—	—

**Chaoborus americanus* larvae also present.

Table 54. Numbers of *Chaoborus cooki* immatures collected 32 km west of Edson, Alberta.
‡ symbolizes dry conditions.

DATE	LARVAL INSTARS				PUPAE		PUPAL EXUVIAE	
	1	2	3	4	Male	Female	Male	Female
3–VI–1975	1	—	26	31	1	—	—	—
17–VI–1975	—	—	—	4	1	—	—	—
27–IV–1976	8	11	—	—	—	—	—	—
18–V–1976	—	2	16	7	—	—	—	—
29–V–1976	—	1	5	3	1	3	—	—
9–IX–1976	—	—	—	—	—	—	—	—
8–X–1976								
11–XI–1976								
1–I–1977								
27–IV–1977	—	1	—	—	—	—	—	—
*8–VII–1977	—	—	—	—	—	—	—	—
*29–VII–1977	—	—	—	—	—	—	—	—

**Chaoborus americanus* larvae also present.

Table 55. Numbers of *Chaoborus cooki* immatures collected 1.4 km west of George Lake, Alberta. ‡ symbolizes dry conditions.

DATE	LARVAL INSTARS				PUPAE		PUPAL EXUVIAE	
	1	2	3	4	Male	Female	Male	Female
12–V–1975	—	—	18	20	—	—	—	—
24–IV–1976	—	12	8	—	—	—	—	—
6–V–1976	—	1	19	29	—	—	—	—
13–V–1976	—	1	2	57	1	—	—	—
25–V–1976	—	—	—	—	6	8	—	—
23–VII–1976								
*18–IX–1976	—	—	—	—	—	—	—	—
30–X–1976								

*Seven *Chaoborus trivittatus* and one *Chaoborus americanus* fourth instar larvae collected.

Development and behavior

Adults. — Parma (1971b: 45) described the emergence of adult *Chaoborus flavicans* and *Chaoborus crystallinus*. Most observations of *Chaoborus trivittatus* and *Chaoborus cooki* agree with that description, but the following are additions or differences. Wings are released from the exuviae after the antennae but before the legs become free. Each of the forelegs and midlegs are released one after the other, but the hindlegs are pulled out together. While the hindlegs are being freed, the wings are folded over the abdomen. Emergence, from the time of the dorsal split to complete release from the exuviae is, under laboratory conditions, 44–95 seconds (n=28) for male and 47–92 seconds (n=25) for female *Chaoborus trivittatus* and 39–70 seconds (n=30) for male and 38–51 seconds (n=13) for female

Chaoborus cooki. All adult *Chaoborus trivittatus* emergences in the laboratory occurred during daylight conditions, and those of *Chaoborus cooki* only took place during night. Myconial fluid was released in 5–21 drops. Males and females flew readily after release of at least some of the myconial fluid but, while females flew only a short distance before landing again, males would fly much further. At 20 C both *Chaoborus trivittatus* and *Chaoborus cooki* males completed rotation of their genitalia within four hours.

Males of both species possess at least some mature sperm upon emergence. Differences in ovarial development between teneral females of *Chaoborus trivittatus* and *Chaoborus cooki* are described elsewhere (p. 179).

Chaoboridae are commonly designated as non-biting mosquitoes. However, Cook (1956:6) states that "Chaoborinae (=Chaoboridae) have all structures necessary for piercing and for feeding on fluids". Felt (1904), Pucat (1965) and Theobald (1901a: 62) suggested that adult Chaoboridae feed on plants but these claims were unsupported. Martini (1931) also recognized adults to be capable of feeding but gave no actual observations.

Both mammalian and avian blood have been found in the guts of female *Corethrella brakeleyi* (Coquillett) and *Corethrella wirthi* Stone (Williams and Edman, 1968). Miyagi (1974) reported the presence of a blood meal of unknown origin in the gut of a female *Corethrella japonica* Miyagi. Its mandibles and hypopharynx are serrated, as are those of female *Corethrella brakeleyi*, *Corethrella wirthi* and *Corethrella appendiculata* Grabham (Miyagi, 1975). McKeever (1977) has recorded *Corethrella* females feeding on *Hyla* tree frogs and was able to attract adult *Corethrella brakeleyi* to a tape recording of frog calls.

Jenkins and Knight (1950) reported an adult male *Eucorethra underwoodi* probing or feeding at pistillate flowers of willow.

Adult *Mochlonyx cinctipes* (Coquillett) did not feed on proffered prunes, raisins, honey-water, or wild flowers, although imbibition of water was observed in the field (O'Conner, 1959). *Mochlonyx velutinus* (Ruthe) took diluted honey (James, 1957).

Some workers have reported on adult life span of chaoborids (summarized by Borkent 1978a: 162) but most, unfortunately, do not report their experimental conditions.

While collecting adult *Chaoborus trivittatus* 2.4 km west of Edmonton, Alberta, on May 13, 1975, I observed that male and female adults often alighted on the pond surface and applied their mouthparts to the water for about 30 seconds, rested for a short period, and then flew away. Air temperature was 17 C. In addition, two males alighted on the ground and walked with their front legs moving alternately in sweeping motions similar to that described by Downes (1974) for adult chironomids searching for honeydew. At this time of year no aphids were present to provide this source of nutrition. Adults commonly exhibit this searching behavior under laboratory conditions if kept in sealed mason jars for at least 24 hours without water.

These observations led me to suspect that adults drink water and that this may be an important factor in prolonging adult life span, consequently influencing adult dispersal capabilities.

I carried out a feeding experiment to see if adults drink water and to determine if water uptake affects longevity.

Blue excreta from adults in jars supplied with dyed water showed that both males and females imbibe water. Longevity results are shown in Figures 35A,B. These results were compared statistically using a Duncan's Multiple Range test ($p < 0.05$) and it was found that: 1) there is no significant difference in longevity between males or females given either clear or dyed water; 2) males which could not drink lived for a significantly shorter period than males which could drink; 3) females which could not drink lived for a significantly shorter period than females with dyed water; and 4) although there was no

significant difference between females without access to water and those with clear water, this is explained by the low numbers in each treatment. Comparison of females without access to water to combined results of females with dyed or undyed water available, using a T-test, revealed them to be significantly different at the 98% level.

These results show that *Chaoborus trivittatus* adults can imbibe water and that this significantly increases their life span. Longevity of adults of most other species may have been seriously underestimated.

During the springs of 1974–1977 I made daytime observations of behavior of *Chaoborus trivittatus* adults 2.4 km west of Edmonton, and 16 km west of Jasper, Alberta. Males were more often seen throughout the emergence periods. They formed columnar swarms ($n=8$) of 1–132 individuals at the periphery of ponds at heights of about 0.3–1.8 m. Females were sedentary on surrounding vegetation, particularly on tree trunks. When disturbed, they flew and were easily seen. However, on May 13, 1975, after 1.5 hours of collecting with an aspirator and aerial net from tree trunks and low vegetation at 2.4 km west of Edmonton, only 32 females were procured. Concurrently, males in swarms were extremely numerous. Similarly, 25 females and 218 males were collected with an aspirator from tree trunks at this locality on May 7, 1977. Female pupae and exuviae, collected May 13, 1975, composed 59.6% ($n=460$) and 40.7% ($n=329$) of a sample respectively. The possibility that the over-abundance of males was due to their earlier emergence, as might be suggested from laboratory rearings, is therefore unlikely.

When females made one of their occasional flights through a male swarm, they were invariably seized front to front by a male. The pair interlocked genitalia and fell immediately to the ground or water surface, where they assumed an end to end position. Matings lasted 51–64 seconds ($\bar{x}=58.7$, $n=5$). Nine other matings observed required a similar period of time but were not measured exactly.

These data suggest the following pattern. Most adult males emerge earlier than females and form large swarms at the periphery of the ponds from which they emerged. Females, after emergence and an unknown period of time, fly through this 'barrier' of males and are mated. Because the sex ratio of emerging adults is nearly 1:1 (Table 51), the far greater proportion of male adults at pond peripheries suggests that females are the main dispersing agent of this species. Well developed ovaries at emergence are probably correlated to the stable habitat which this species inhabits and suggests that *Chaoborus trivittatus* female adults cannot disperse as far with their fully developed eggs as can *Chaoborus cooki* female adults (see below).

If a sex ratio of nearly 1:1, and observations of concentrated male swarms at the periphery of water bodies are alone indicative of this type of adult behavior (i.e., females mated at the pond or lake periphery and subsequently dispersing), observations of adults of the species *Chaoborus sensu stricto* suggest that these exhibit similar behavior. Bradshaw (1973) reported males to compose 57% of populations of *Chaoborus americanus*. I have observed large male swarms of this species at the periphery of numerous ponds near Edmonton, Alberta. Males make up 43–45% of *Chaoborus flavicans* populations (Parma, 1971b) and swarms have been observed at a number of localities (Berg, 1937). Parma (1971b) noted the concentration of male *Chaoborus flavicans* at the periphery of the water bodies he studied. Parma (1971b) reported males to comprise 39–60% of *Chaoborus crystallinus* populations and both he and Nielsen and Greve (1950) have observed male swarms of this species. Neither sex ratio or swarming behavior have been reported for *Chaoborus obscuripes* (van der Wulp). These data suggest that at least three of the four species of *Chaoborus sensu stricto* share a common type of adult reproductive behavior and dispersal with *Chaoborus trivittatus*. The significance of this is discussed in the section on zoogeography and speciation.

I have little data on adult behavior of *Chaoborus cooki* in the field. In 1975 and 1976, at the pond 1.4 km west of George Lake, and in 1976, at the pond 1.6 km south of Jasper, Alberta, emergence of adult

Chaoborus cooki was observed only during the night. Although both New Jersey and CDC light traps were present at the edges of the ponds, adults that emerged were not trapped. Upon emergence, adults flew upward out of the field of vision. On the day after each of the nights I observed emergence, I swept, with an aerial net, all surrounding vegetation for a least 100 m in all directions of both ponds, but with no captures. I also visually examined the immediate area and climbed the trees surrounding the ponds but neither collected nor saw any adults.

Timing of laboratory matings of *Chaoborus trivittatus* adults (45–65 seconds, $n=6$) approximated those observed in the field (see above). This would suggest that timings of matings of *Chaoborus cooki* adults in the laboratory (91–122 seconds, $n=8$) also approximates those under field conditions.

These data, a sex ratio of males to females of about 3–5 to 1 (see p. 193) and retarded ovarian development, indicate that *Chaoborus cooki* adult behavior differs substantially from that of *Chaoborus trivittatus*. This suggests that *Chaoborus cooki* adults do not remain near the pond from which they emerge and both males and females disperse. This behavior would ensure the survival of at least part of the total population. Temporary ponds which became dry before adult emergence would undoubtedly kill the immatures present.

Female adults probably exhibit underdeveloped ovaries on emergence so that fat body can be used as energy for flight should a suitable habitat not be located and would guarantee at least the production of a few eggs once a suitable habitat is found (Roff, 1977).

Lack of records of adults in the area from which they just emerged suggests that the adults mate after a period of dispersal. Greater numbers of males than females would be more conducive to successful mating after dispersal and might explain the inequality in numbers of males and females.

Differences in dispersal capabilities and behavior of *Chaoborus trivittatus* and *Chaoborus cooki* concurs with the suggestion by Southwood (1962) that, generally, species found in unstable habitats show more intensive dispersal behavior than do those in more stable habitats. For species of *Chaoborus*, degree of ovarian development in teneral adults (Fedorenko, 1975c; Parma, 1971b) and number of eggs per female (Fedorenko, 1975c; McGowan, 1974; Parma, 1971b; Sikorowa, 1973) is also correlated to stability of habitat.

Egg rafts of *Chaoborus trivittatus* are laid in a similar way to those of *Chaoborus flavicans* and *Chaoborus crystallinus* (Parma, 1971b: 28). I have observed oviposition in the field during daylight hours, but did not measure the rate of egg laying.

I have no observations of oviposition by females of *Chaoborus cooki*.

Eggs. – Egg rafts of *Chaoborus trivittatus*, like those of species of *Chaoborus sensu stricto* (McCloy, 1950 (as *Chaoborus crystallinus* = *Chaoborus americanus*); Parma, 1971b; Sikorowa, 1973) are in the form of floating discs with the eggs arranged in a spiral. My observations of egg rafts and egg development are similar to those reported by Parma (1971b: 30). I found many egg rafts stuck to floating debris at the water surface. Eggs in the laboratory turn dark brown after one or two days. The pharate first instar larvae were positioned as shown by Parma (1971b: fig. 12) for *Chaoborus flavicans*. As Parma (1971b: 29) has pointed out, oviposition can be disrupted; thus I did not consider number of eggs per raft to be a significant measurement. I have found an egg mass, for example, of *Chaoborus trivittatus* composed of nine eggs. This clearly does not reflect the number of eggs per female (p. 179) and therefore cannot be used to interpret interspecific or intraspecific variation.

Eggs of *Chaoborus cooki* were obtained only from laboratory mated females. These were laid in a semispherical mass on walls of vials, which were used to retain adults. The eggs were held together by minute amounts of gelatinous matrix. The exochorion of each individual was also sticky. Endochorions of fertilized eggs turned dark brown within two to three days. The endochorion of non-fertilized eggs turned slightly brown in places.

I attempted to collect eggs of *Chaoborus cooki* from the site 1.4 km west of George Lake, after the pond had become dry on October 30, 1976, when the surface soil was frozen to a depth of about one to three centimeters. Soil samples were taken from each of 50 by 50 cm grids on the entire area covered by the high water mark of the temporary pond. When *Typha* sp. stems were present in a grid a sample was taken of these, cut off below the soil surface. In addition, samples of brush that immediately surrounded the pond were taken. In the laboratory soil samples were sieved and vegetation scanned under the binocular microscope. Nine soil samples were treated with floatation techniques using NaCl. I was unable to retrieve any eggs or egg shells.

I have observed hatching of eggs only for *Chaoborus trivittatus* from 2.4 km west of Edmonton, and 16 km west of Jasper, Alberta. The events of hatching were similar to those described by Parma (1971b: 32). Eggs of *Chaoborus trivittatus* hatch within three days, usually all of one egg mass hatching within a few hours. A few eggs were sieved from a bottom sample taken from a pond 16 km west of Jasper, Alberta, on June 18, 1976, after the adult emergence period was completed. All eggs were white, suggesting that they were not fertilized, and by June 24, 1976, all had deteriorated in the laboratory. Outer eggs on the egg raft hatch first. Egg shells of *Chaoborus trivittatus* split longitudinally and the posterior part of each larva is freed. A few were caught with their head capsule stuck in the egg shell but most, with violent struggling, freed themselves. Unlike the egg shells of *Chaoborus crystallinus* and *Chaoborus flavicans* (Parma, 1971b: fig. 13), and *Chaoborus americanus* (pers. obs.), in which the egg shell on each side of the longitudinal slit folds inwards, the sides of the egg shell of *Chaoborus trivittatus* fold outward (Fig. 9D). This unique character may have evolved to compensate for the large size of *Chaoborus trivittatus* first instar larvae and therefore allow for fewer numbers of first instar larvae being stuck in the egg shell.

All eggs of *Chaoborus trivittatus* collapsed under atmospheric conditions and therefore are not resistant to desiccation.

Eggs of *Chaoborus cooki* do not hatch within a few days, as do those of other *Chaoborus* species (Deonier, 1943; Herms, 1937; McGowan, 1974: 498; Sikorowa, 1973: 76). Endochorions of these eggs, white when laid, become extremely dark brown within 2–3 days. Larvae develop to at least a stage where head capsule and air sacs are visible, but do not hatch at 20 C. After three months at this temperature, and an L:D photoperiod of 18:6, some eggs were treated with either three successive floodings, three days apart, of deoxygenated water, or one treatment with xylene vapor, but they failed to hatch. Other eggs were treated to 20 C temperatures and an L:D photoperiod of 18:6 for two months, 2 C and total darkness for four months and then returned to former conditions but with no evidence of hatching. A few eggs did hatch after being kept at 20 C and an L:D photoperiod of 18:6 for two months and then total darkness at 2 C for ten months. Study of the egg shell showed that the exochorion was gone (as it was in some unhatched eggs), and the chorion had split to release the larva in a way different (Fig. 9E) to that described for other species.

Eggs of *Chaoborus cooki* were treated to one month of atmospheric conditions without collapse. The thick exochorion is apparently a protective layer against desiccation. The highly sculptured exochorion probably functions as a plastron under alternately dry and wet conditions (Hinton, 1969; Hinton and Service, 1969).

Larvae. – I observed horizontal clumping of second, third, and fourth instar larvae in ponds which were not entirely shaded from direct sunlight. Clumping was related to presence of shade provided either by surrounding vegetation, topographical features, or emergent aquatic vegetation. This is clearly a factor which influences sampling results of *Chaoborus trivittatus* and *Chaoborus cooki* larvae from shallow water bodies. For example, a pond measuring about 5 by 14 m, 7.6 km northwest of Mountain Park, Alberta, was sampled successively with a dip net along the north side and a portion of the south

side which were exposed to direct sunlight, without collecting a single larva. A prominent boulder on the south shore provided shade in part of the pond and in this region I collected 109 fourth instar larvae of *Chaoborus trivittatus* in a single sweep of the net.

Similar response to shade is probably exhibited by *Chaoborus pallidus* (Akehurst, 1922: 352; Edwards, 1920; Sikorowa, 1964)

This factor is probably one which influences the restriction of *Schadonophasma* species to woodland conditions. In addition, it is possible that this response to shading is a modification of the response to light which is important in vertical migration of some *Chaoborus* species (Chaston, 1969; LaRow, 1968, 1969).

I observed grooming behavior of fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Larvae often lashed at the posterior portions of their bodies with their antennae and mandibles. Occasionally larvae place the posterior portion of the abdomen in their oral cavity, the anal fan completely in the mouth. Even the slightest disturbance resulted in return to a normal position. However, on one occasion I observed a larva of *Chaoborus trivittatus* keep its tail end in its mouth for over 2.5 hours. This behavior is undoubtedly an important adaptation for removal of epibionts.

I did not observe larvae of *Chaoborus trivittatus* or *Chaoborus cooki* bury themselves in the bottom substrate in aquaria, although, when disturbed, they would dart toward the bottom and often cling with mouthparts to bottom debris.

Although differences in prey type were evident between *Chaoborus trivittatus* and *Chaoborus cooki*, I did not quantify this information because of biases produced by preservation techniques (Swift and Fedorenko, 1973). Although Fedorenko (1975a, 1975b) and Swift and Fedorenko (1975) have recorded the diet of *Chaoborus trivittatus* fourth instar larvae, from an oligotrophic lake in southwestern British Columbia, as composed of copepods and cladocerans, it is not known to what extent another habitat, such as a pond, affects prey type. For example, I observed *Chaoborus trivittatus* fourth instar larvae capturing chironomid larvae. I did not find ostracod remains in the gut of *Chaoborus trivittatus* fourth instar larvae and, in the laboratory they lashed out at, but rejected ostracods as food. Contrary to this I found numerous *Chaoborus cooki* larvae with ostracods in their crops. Chironomid and, in *Chaoborus cooki* larvae from some ponds, culicid larvae were also common. To a certain degree, differences of prey type must reflect habitat differences, but these observations of ostracod ingestion suggest species differences in ability to ingest at least this prey type.

Male larvae of both species pupate earlier than do female larvae (Table 51, 56). *Chaoborus cooki* larvae have a more extended pupation period than do those of *Chaoborus trivittatus* under laboratory conditions.

Pupae. — Pupation of individuals of *Chaoborus* species has not previously been observed. The following is derived from observations of a single pupation for each of *Chaoborus trivittatus* and *Chaoborus cooki*. Under laboratory conditions pupation required about two or three seconds. The fourth instar larva suddenly contracted along its entire body length in a quivering motion. The larva turned into a vertical position, the pupal horns popped through the thoracic suture, followed by the thorax and head of the pupa. The larval exuviae slipped down the length of the pupal abdomen and was thrown off the tip by a forward flick of the abdomen.

Parma's (1971b: 38) description of macroscopic color changes during pupal development also apply to pupae of *Chaoborus trivittatus* and *Chaoborus cooki*.

Under laboratory conditions, the pupal period of *Chaoborus trivittatus* is three (n=1) to four (n=85) days for males and four (n=22) to five (n=4) days for females. The pupal period of male *Chaoborus cooki* lasted two to six days (n=1,2,6,28,21 respectively), and of females three to seven days (n=1,13,13,11,4 respectively).

Table 56. Numbers of pupae resulting from 42 individually reared fourth instar larvae of *Chaoborus cooki* collected 32 km west of Edson, Alberta. Pupation recorded only on dates presented.

DATE	NUMBER OF PUPAE	
	Male	Female
5-VI-1975	0	0
6-VI-1975	4	0
9-VI-1975	25	2
13-VI-1975	2	7
16-VI-1975	1	0
20-VI-1975	1	0
Total:	33	9

Differences in development of ovaries between pupae of *Chaoborus trivittatus*, *Chaoborus cooki* and *Chaoborus nyblaei* are described elsewhere (p. 179).

To compare the sex ratio of *Chaoborus trivittatus* and *Chaoborus cooki* I collected fourth instar larvae before any indication of pupation in the field, from 2.4 km west of Edmonton and 32 km west of Edson, Alberta (not the same locality from which the life cycle of *Chaoborus cooki* was studied), respectively. Individual rearings of 44 larvae of *Chaoborus trivittatus* produced 23 male and 21 female pupae and 42 *Chaoborus cooki* larvae produced 33 male and nine female pupae. The use of a compound character index to sex fourth instar larvae of *Chaoborus cooki* (p. 161), from 1.6 km south of Jasper, indicated a sex ratio of 52 males to 10 females.

MATING EXPERIMENTS

Observations of forced matings in the laboratory between members of two populations give indications of their reproductive compatability and, therefore, their conspecificity. I tested my interpretation of morphological, bionomic and temporal discontinuities as indicative of the presence of two species of *Schadonophasma* in North America by attempting to cross individuals of *Chaoborus trivittatus* and *Chaoborus cooki*.

Results of crossing (Table 57) show several important features. Crossings of male *Chaoborus trivittatus* and female *Chaoborus cooki*, as compared to intraspecific crossings, showed reduced number of eggs, number of fertilized eggs, and reduced fertility. Four of the six crosses resulted in no eggs being laid. Reduced fertility and low number of eggs from some of the intraspecific crosses must be the result of experimental conditions.

Crosses between male *Chaoborus cooki* and female *Chaoborus trivittatus* resulted in no eggs. It was apparent during the crossings that male *Chaoborus cooki* had difficulty in coupling with the female genitalia. In an additional six attempted couplings the penis valves of male *Chaoborus cooki* could not insert into the female genitalia of *Chaoborus trivittatus* and copulation did not take place. This may be due to the more bulbous nature of the head of penis valves of *Chaoborus cooki* which may not fit into the proper receptacle of the female genitalia.

These observations indicate that reproductive isolation between *Chaoborus trivittatus* and *Chaoborus cooki* is additionally maintained by mechanical and genetic incompatibilities.

Table 57. Results of intraspecific and interspecific crossings of adult *Chaoborus trivittatus* and *Chaoborus cooki*.

Species crosses (♂ X ♀)	Couple No.	No. of Eggs	%Fertile
TRIV. X TRIV.	1	190	98.4
	2	133	71.3
	3	27	77.8
	4	180	60.0
	5	171	97.1
COOKI X COOKI	1	78	61.5
	2	72	86.1
	3	73	88.7
	4	70	70.4
	5	0	0
COOKI X TRIV.	1	0	0
	2	0	0
	3	0	0
TRIV. X COOKI	1	85	11.8
	2	65	0
	3	0	0
	4	0	0
	5	0	0
	6	0	0

PHYLOGENY AND ZOOGEOGRAPHY

Phylogenetic and zoogeographic considerations are logical conclusions to systematic studies. In this section I give my working principles for such considerations, evidence for the recognition of three species of *Schadonophasma*, and hypothesize their evolutionary history. Because the evolution of species of *Schadonophasma* can be best understood in the context of ex-group comparisons I also consider the evolution of the genus *Chaoborus*.

In recent years there has been much debate concerning the principles and methods of cladistic analysis as used to infer phyletic relationships (e.g. Ashlock, 1974; Brundin, 1972; Darlington, 1970; Griffiths, 1972, 1974; Hull, 1970; Mayr, 1974; Schlee, 1975; Sneath and Sokal, 1973; Sokal, 1975; and papers cited in these). Although adherence to methods themselves can blind investigators to more reasonable alternative interpretations (Darlington, 1970), Hennigian principles (see Kavanaugh, 1972) have broad applicability in the determination of evolutionary relationships. I have, therefore, used them to infer the evolutionary history of species of the genus *Chaoborus*.

One potential source of error in the application of cladistic analysis concerns the weighting of characters on a superficial basis. Hecht and Edwards (1977) and Szalay (1977) have discussed the importance of detailed investigation of individual characters used in phylogenetic analysis. Although this may not be possible in many studies, this investigation provided a basis from which to better interpret the evolutionary significance of most characters used and therefore improved the use of cladistic techniques. These data allowed a more probable interpretation of the evolution of some *Chaoborus* species and, in particular, of the species of *Schadonophasma*.

Most systematic studies, some because of a lack of bionomic information, only consider allopatric speciation as the means of evolution of lineages. In a recent study Tauber and Tauber (1977) have proposed a genetic model for sympatric speciation of more general applicability than that proposed by Bush (1975a, 1975b). However, most studies suggesting interpretations of sympatric speciation lack study of the phyletic relationships between the organisms concerned. My interpretation of possible speciation events in the history of *Schadonophasma* species provides an example of how phyletic relationships and zoogeographical considerations may give supportive evidence for inferring an allopatric or sympatric speciation model.

Darlington (1970: 3) has criticized assumptions of dichotomous speciation and described several situations in which branching was possibly polychotomous. I have not found evidence of trichotomous speciation of the three species of *Schadonophasma*. The presence of synapomorphies for two of the species supports only dichotomous speciation in the history of *Schadonophasma* species.

Evidence and Recognition of three species of *Schadonophasma*

The basic taxonomic unit used for inference of phylogenies is the species or species group. A phylogeny therefore depends on correct interpretation of the diversity it attempts to explain. The following is a discussion of evidence for the recognition of three species of *Schadonophasma*.

Morphological, bionomic, developmental and behavioral incongruities, as well as differences in geographic variation and distribution among groups of populations, are logical criteria for recognition of species if the biological species concept is accepted as a testable hypothesis. Only experimental tests of reproductive incompatibilities, however, might provide direct evidence of reproductive isolation. It is the concordance of such indirect and direct evidence of reproductive isolation that allows systematists to interpret the former as the result of such reproductive isolation. The results of this study, as do many others, confirm the validity of this assumption.

From the results of this study I consider discontinuities in the following features to support my conclusion that there are two species of *Schadonophasma* in North America recognizable as *Chaoborus trivittatus* and *Chaoborus cooki*:

1. Structure of eggs, all stages of larvae, pupae and adults
2. Pattern of development of LB/AL from first through fourth instar larvae.
3. Characters of fourth instar larvae which are sex-associated in one species but not the other.
4. Correlations of characters of fourth instar larvae.
5. Patterns of geographical variation of characters of fourth instar larvae in Alberta.
6. Rates of development of eggs, larvae and ovaries of adults.
7. Life cycle and types of habitat commonly occupied.
8. Larval prey type.
9. Adult behavior.
10. Reproductive compatibilities, when adults from different populations were crossed in the laboratory.
11. Lack of sympatry in western and eastern coastal regions of the United States.

I do not have nearly the same amount of evidence to justify recognition of the third species, *Chaoborus nyblaei*, in Fennoscandia. Because of similarity of compared semaphoronts, I assumed that all specimens from Fennoscandia were conspecific. Adult material collected 2–3 km SW of Nuorgam,

Finland, on July 24, 1960, was probably conspecific with larval and pupal material collected there.

Most characters of the immatures and color of adults of *Chaoborus nyblaei* are similar to those of *Chaoborus cooki*. However, shape of the adult male penis valve and prelabral appendage of fourth instar larvae are most similar to those of *Chaoborus trivittatus*. This combination of features suggests the presence of a third species, and this is further supported by extremes of variation of certain characters of the fourth instar larvae of *Chaoborus nyblaei* (number of mandibular fan bristles and anal fan setae).

Because of difficulties in interpreting morphologically similar, allopatric populations separated by a geographical area from which specimens are not known (Mayr, 1969), it is impossible to be certain that *Chaoborus nyblaei* is a separate species. Therefore it might be conspecific with either *Chaoborus trivittatus* or *Chaoborus cooki*. Overall morphological similarity would indicate, if this were so, that *Chaoborus nyblaei* and *Chaoborus cooki* are conspecific. However, patterns of geographical variation of *Chaoborus cooki* would not suggest that the higher mean values of number of anal fan setae, and lower mean value of number of anal fan setae of the larvae of *Schadonophasma* in Fennoscandia are the result of variation of those characters of *Chaoborus cooki*. Nevertheless, the possibilities of character displacement producing such features as exhibited by the population in Fennoscandia cannot be presently negated. Further study of *Chaoborus nyblaei* populations to complement the data given in this study for *Chaoborus trivittatus* and *Chaoborus cooki*, further investigation of the range of *Chaoborus nyblaei* and detailed analysis of geographical variation of *Chaoborus nyblaei* and *Chaoborus cooki* once further samples become available, would give further clues to questions of conspecificity. Notwithstanding, it is probable that the Bering Strait area is devoid of *Schadonophasma* populations and presents at least a recent barrier between North American, and should they exist, eastern Asian populations of *Schadonophasma*.

Phylogeny of *Chaoborus*

Saether (1970), using cladistic methods, proposed a phylogeny of *Chaoborus* species and chaoborid genera but dealt only with those of the Holarctic region. He used 29 characters to determine relationships among subgenera of *Chaoborus*. However, his interpretation of the polarity of many of these characters is questionable.

A number of characters are used by Saether (1970), for which he gives no criteria for determining the apomorphic and plesiomorphic ends of the morphoclines and for which there are none apparent (Maslin, 1952). For example, the character HW/WBE is considered plesiomorphic if 2.5–4.2 and apomorphic if 1.5–1.8. However, the closest sister group to *Chaoborus* for which these data are available is *Mochlonyx* which, if all species are considered, has a total range of 1.8–2.4 (Cook, 1956). If this feature represents the plesiomorphic condition of *Chaoborus*, both ends of the morphocline recognized by Saether would be apomorphic. However, HB/WBE ratio of male adult *Eucorethra underwoodi* is 8.3–8.5 (Cook, 1956) and this may also reflect plesiomorphy. Until further ex-group comparison has been made, phylogenetic interpretation of this character is conjectural.

It is also not clear how Saether interpreted the polarity of morphoclines of values of Y/R_3 and Y/X of adults (males?), width/length of abdominal segment VII of pupae and AS/AL of larvae, when these data were available only for some species of *Chaoborus*.

It is well known that character states which involve loss of a feature are particularly suspect of convergent or parallel evolution (e.g. it could be as likely for species to independently lose features as for a single ancestor of species to do so). Interpretation of the following character states as synapomorphic provides at best an uncertain basis for reconstructing a phylogeny: loss of parascutellar setae and reduction of number of mesepimeral and pronotal seta of adults; loss of color of the pupal paddle membrane; reduction of the relative length of the median rib of the pupal paddle; and reduction of the

larval tentorium.

Shape of the apex of the male adult gonostylus and loss of a pair of larval labral setae are autapomorphies for *Chaoborus pallidus*, and cannot be used to determine relationships between species or groups of species.

Saether (1970: 47, Trend 46) considered the placement of the simple seta toward the apex of the median rib of the pupal paddle to be apomorphic within *Chaoborus*. This condition, however, most closely approximates the condition featured by *Mochlonyx* and *Eucorethra* pupae suggesting that it is more likely to be the plesiomorphic character state.

Following Saether's (1970) publication, larvae of some African species have been well described (Green and Young, 1976; McGowan, 1972, 1976). In addition, Saether (1976) has redescribed adults, pupae and fourth instar larvae of *Chaoborus brasiliensis* (Theobald) and *Chaoborus magnificus* Lane from Venezuela. Using these descriptions and my own observations, I have constructed a phylogeny of those species of *Chaoborus* for which sufficient information is available. The characters used and interpretation of their plesiomorphic and apomorphic states are given in Table 58. All character states were judged plesiomorphic or apomorphic on the basis of ex-group comparisons (especially *Mochlonyx* and *Eucorethra*) with the exception of prelabral appendage shape. The interpretation of several characters requires special comment.

Two characters used are interpreted as apomorphic in their reduced state: relative length of the median rib of the pupal paddle and, relative degree of sclerotization and size of the larval tentorium. These were used because of a shortage of characters in this analysis. As proposed here, reduction of the larval tentorium has occurred twice.

The prelabral appendage of *Chaoborus* larvae is undoubtedly a seta (Balvay, 1977c). Although it is not known which seta of other chaoborids is homologous to this prelabral appendage, it is reasonable to assume that ontogenetic development of the prelabral appendage from a simple seta in the first two instars of all *Chaoborus* species to a laterally flattened appendage in the last two instars of some species, corresponds to the evolution of these setae (Akehurst, 1922: 352).

The only clues for determining the polarity of AS/AL of *Chaoborus* larvae are provided by the larvae of *Mochlonyx velutinus* and *Eucorethra underwoodi*. *Mochlonyx velutinus* fourth instar larvae possess an antennal seta near to the base of the antenna but none were measured exactly. The AS/AL of three fourth instar larvae of *Eucorethra underwoodi* was 0.51–0.59 (mean=0.558). In the construction of the phylogeny I have used this feature only to interpret the extreme values of AS/AL of *Schadonophasma* as apomorphic. Change of this ratio, from a low value in first instar larvae to a high ratio in fourth instars (Fig. 22A), would support such an interpretation.

The polarity of two characters, coloration of adult legs and state of the larval dorsal process, has apparently been misinterpreted by Saether (1970). He suggested that ringed legs of adults is a plesiomorphic state. This is probably only partially true. Although bases and apices of leg segments and articles are dark in a number of ex-groups, and is therefore probably plesiomorphic, spotted femur and tibia of legs of some African species of *Chaoborus* (Verbeke, 1958), and some species of the subgenus *Sayomyia* (e.g. *Chaoborus punctipennis*, *Chaoborus astictopus*, (per. obs.) *Chaoborus brasiliensis*), is probably apomorphic.

Saether (1970: 50) also considered the two segmented dorsal process of the fourth instar larvae of some *Chaoborus* species to be the plesiomorphic condition for the genus and implies (Trend 67) that the dorsal process is actually the evolutionary vestige of the respiratory siphon. However, as pointed out by Cook (1956: 14) 'the annulation on which this "siphon vestige" occurs has a musculature which indicates that it is a segment. This then is segment 9, and the siphon occurs on segment 8. Thus, the term "siphon vestige" seems to be inaccurate'. In addition, Parma (1971a) followed the shape of the dorsal

Table 58. Characters and character states within the genus *Chaoborus*.

Character	Plesiomorphic	Apomorphic
<i>Adults.</i>		
1. Leg coloration	Pigmented only at bases and apices of leg segments and tarsal articles	Femur and tibia ringed or spotted along their lengths
2. Wing coloration	Spotted	Not spotted
3. Gonocoxite shape	No protuberance on inner face	Protuberance on inner face
4. Penis valve	No apical claw when head rounded	Apical claw and rounded head
5. Comb-like setae on 3rd metatarsomere of female	Absent	Present
<i>Pupae</i>		
6. Median rib of pupal paddle	Straight at apex	Curved at apex
7. Median rib of pupal paddle	Extended to edge of paddle	Not extended to edge of paddle
<i>Larvae</i>		
8" Prelabral appendage	Setose; covered with spines	Broadened with spines directed anteriorly and posteriorly
8"" Prelabral appendage	Broad with spines directed anteriorly and posteriorly	Broad with spines directed only anteriorly
8''' Prelabral appendage	Broad with spines directed anteriorly and posteriorly	Setose but with spines directed only anteriorly and posteriorly
9. Antenna	Not curved at posterior base	Curved at posterior base
10. Dorsal Process	No article present	Single article present
11. Tentorium	Strongly sclerotized and thick	Weakly sclerotized and thin
12. Subordinate Mandibular Tooth	Not spinose	Spinose
13. AS/AL	Lower value	Higher value

process from instar to instar of *Chaoborus flavicans* and found the pointed dorsal process to be present only in the later instars. If this feature represents the siphon vestige, one would expect it also to be present in earlier instars. I further tested this hypothesis by examining the position of the tracheal trunks of fourth instar larvae of *Chaoborus cooki*. I found that thawing previously frozen larvae resulted in the trachea filling with gas, allowing them to be clearly observed. The tracheal trunks showed a notable dorsal bend in the eighth abdominal segment (Fig. 8D) similar to the dorsal bend of the tracheal trunks of *Mochlonyx* larvae into the siphon (Montchadsky, 1953: fig. 1).

These observations indicate that the small dorsal article of the ninth abdominal segment of larvae of some *Chaoborus* species is in fact a newly evolved feature and not the vestige of the respiratory siphon. Absence of such an article is therefore the plesiomorphic condition. The pointed dorsal process exhibited by *Chaoborus flavicans* and *Chaoborus crystallinus* fourth instar larvae is also probably an independently derived characteristic.

The most probable phylogeny of species of *Chaoborus*, using the characters in Table 58, is presented in Figure 36. I accept Saether's (1970) conclusion concerning the phyletic relationships between the four species of *Chaoborus sensu stricto*. This phylogeny differs from that hypothesized by Saether (1970,

1976) primarily in considering *Chaoborus albatus* as possibly the sister species of *Chaoborus magnificus* and these species plus *Chaoborus brasiliensis*, *Chaoborus punctipennis*, and *Chaoborus astictopus* (hereafter designated as 'ambpa') the sister group of *Schadonophasma* plus *Chaoborus sensu stricto*. The placement of *Chaoborus pallidipes* is uncertain. This species could equally well be the sister group of *Schadonophasma* plus *Chaoborus sensu stricto*, or of the species group 'ambpa'.

The grouping of *Chaoborus anomalus*, *Chaoborus ceratopogones*, and *Chaoborus pallidus* is tentative. These are recognized as monophyletic on the basis of leg coloration which, as here hypothesized, shows convergence with the species group *Chaoborus brasiliensis*, *Chaoborus punctipennis*, and *Chaoborus astictopus*. Any of *Chaoborus anomalus*, *Chaoborus ceratopogones* or *Chaoborus pallidus* could be considered a sister group of the species group 'ambpa' if the following events are assumed to have occurred: 1) the basal curvature of the larval antenna was secondarily lost in these species, or the curvature evolved independently in species groups 'ambpa' and *Schadonophasma* plus *Chaoborus sensu stricto*; and 2) *Chaoborus albatus* and *Chaoborus magnificus* secondarily lost the derived coloration of adult legs. However, these events provide a less parsimonious explanation than does the convergence of leg coloration as presented here. Similarly the development of a lobe on the inner face of the gonocoxite of both *Chaoborus anomalus* and the species group *Chaoborus brasiliensis*, *Chaoborus punctipennis*, and *Chaoborus astictopus*, is considered a result of convergent evolution.

A character which may be synapomorphous for *Chaoborus anomalus*, *Chaoborus ceratopogones* and *Chaoborus pallidus*, except for which observations were not available for all other species, is the basally swollen and highly curved postantennal filaments (Saether, 1970: fig. 6C). Verbeke (1958: 43) also considered *Chaoborus ceratopogones* and *Chaoborus pallidus* to be closely related on the basis of similarity of adults, pupae and larvae.

Although the broadening of the prelabral appendage may have evolved independently four times, I here consider it to have occurred only once. The setose appearance of the prelabral appendages of *Chaoborus punctipennis* and *Chaoborus astictopus* is therefore a derived state and is only superficially similar to the primitive condition. This explains why the setaceous prelabral appendages of these two species have spines directly only anteriorly and posteriorly.

Fossil evidence

The study of fossils can give important evidence for the correct interpretation of the evolutionary history of a group of extant organisms. However, few systematists studying arthropods are fortunate to have such fossils available to them.

A number of authors have described or mentioned *Chaoborus* subfossils (Alhonen and Haavisto, 1969; Deevy, 1942; Frey, 1955, 1962, 1976); Goulden, 1966a, 1966b; Hofmann, 1971, 1978; Marland, 1967; Stahl, 1959, 1969) or fossils (Borkent, 1978b; Edwards, 1923; von Heyden, 1862; Hope, 1847; Meunier, 1904; Scudder, 1890 (questionable identification); Serres, 1829: 268). Most of the fossil material is in need of redescription. I examined the fossil pupa and disarticulated pupal parts described by von Heyden (1862) as *Culicites* (= *Chaoborus*) *tertiarius* and have published (Borkent, 1978b), a redescription of those fossils and of some larval fragments (mandibles and anal fans) also present on the brown, paper-coal. The pupal paddles exhibit median ribs which extend to the edge of the paddle and are curved apically. In addition the subordinate tooth at the base of the two larger teeth of some of the larval mandible is very similar to that of *Chaoborus flavicans*. It is not certain that the larval fragments are from the same species as the pupa and pupal parts. Nevertheless, mandible structure suggests that they are from a population conspecific with *Chaoborus flavicans* (*Chaoborus sensu stricto*), or from a species which is the sister species of *Chaoborus flavicans*. The apical curvature of the median rib of the pupal paddles is a synapomorphous character which serves to group *Schadonophasma* and *Chaoborus sensu*

stricto. Although I cannot confidently place the fossil pupa or pupal parts with one of these lineages, it is clear that if convergence has not taken place this species shares a common ancestry with, or within, either of these two subgenera.

According to Mägdefrau (1968), Edwards (1923) correctly determined the age of the fossils as Upper Oligocene. This would indicate that speciation giving rise to *Chaoborus flavicans*, and its sister species *Chaoborus crystallinus*, took place at least 25 million years B.P., and that the speciation event which gave rise to the lineages represented by extant species of *Schadonophasma* and *Chaoborus sensu stricto* took place before that time.

The finding of these fossils at Rott, Siebengebirge, West Germany is consistent with a hypothesis that the species group of *Schadonophasma* plus *Chaoborus sensu stricto* evolved under temperate conditions (Mägdefrau, 1968).

Phylogeny of *Schadonophasma*

Saether (1970) proposed a phylogeny for the species of *Schadonophasma* based on six characters. I have already discussed the difficulties of interpretation of four of these (number of mesepimeral and pronotal setae; ratio of Y/X; WS/LS; shape of dorsal process). Saether's phylogenetic interpretation of variation of the penis valve shape seems to be correct for *Schadonophasma*. The interpretation of body size variation is probably incorrect but is discussed below.

Although the phylogeny I propose for the species of *Schadonophasma* is identical to that of Saether (1970), except for his consideration of *Chaoborus brunskilli* (= *Chaoborus trivittatus*) as the sister species of *Chaoborus trivittatus*, my approach to the problem is substantially different. For the analysis I have chosen seven characters (Table 59), some of which are discussed below.

Table 59. Characters and character states within the subgenus *Schadonophasma*.

Character	Plesiomorphic	Apomorphic
<i>Adults.</i>		
1. Penis valve	Apical claw short	Apical claw elongate
<i>Fourth Instar Larvae</i>		
2. Head capsule length	Smaller	Larger
3. AS/AL	Lower value	Higher value
4. Prelabral appendage	Elongate	Broad
5. Number of mandibular bristles	Lower	Higher
6. Number of anal fan setae	Lower	Higher
<i>Eggs</i>		
7. General structure	Thin exochorion; no pattern on surface of exochorion	Thick exochorion; polygonal pattern on surface of exochorion.

Saether (1970: 43) in Trend 2, recognized the largest chaoborid, *Eucorethra underwoodi* to represent the plesiomorphic condition and the smallest, the apomorphic condition. He therefore considers the large size of *Schadonophasma* spp. and within the subgenus *Chaoborus cooki* and *Chaoborus nyblaei*, to be plesiomorphic. However, his determination of polarity of this morphocline is almost certainly incorrect.

Schadonophasma species are the largest of all described *Chaoborus*, and are larger than all species of *Cryophila* Edwards, *Mochlonyx*, *Promochlonyx* Edwards, and *Australomochlonyx* Freeman; genera to which *Chaoborus* is more closely related than to *Eucorethra*. It is almost certain therefore that the large size of *Schadonophasma* members as a group, and those of *Chaoborus cooki* and *Chaoborus nyblaei* in particular, represents an apomorphic condition. In this presentation I have used larval head capsule length to represent the overall size of the species.

I have already discussed above the interpretation of AS/AL and prelabral appendage shape.

The high number of mandibular fan bristles of some members of *Chaoborus trivittatus* probably represents the apomorphic end of a morphocline. *Mochlonyx* fourth instar larvae have six to seven bristles in the mandibular fan (Cook, 1956; O'Conner, 1959), and no other *Chaoborus* species have members exhibiting such large numbers of mandibular fan bristles.

Some fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki* and all those of *Chaoborus nyblaei* have a larger number of anal fan setae than other *Chaoborus* species. *Mochlonyx* fourth instar larvae have 28–30 anal fan setae, *Eucorethra underwoodi* has 32 (Cook, 1956). These ex-group comparisons would suggest that only the high number of anal fan setae of *Chaoborus cooki* and *Chaoborus nyblaei* are apomorphic. However, some evidence suggests that the evolution of changes in number of anal fan setae is more complex. From observations of the swimming behavior of *Chaoborus* larvae it is clear that the anal fan functions as a fulcrum against which the larvae can produce a forward motion. It would seem reasonable therefore to suggest that if there are developmental restrictions on the size of individual anal fan setae, the number of anal fan setae may be related to the size of the species and that these two characters coevolved. Distribution of number of anal fan setae, relative to range of head capsule length for species of *Chaoborus* for which these data are available (Fig. 37), would support this hypothesis. These two characters would generally, therefore, not give independent evidence of phyletic relationships. However, it is also apparent from Figure 37 that the relationship is not a constant one. Although this may be due to inadequate sampling for some species, it is probable that other factors are important in the evolution of number of anal fan setae. For example, even though there is no significant difference in head capsule length of *Chaoborus cooki* and *Chaoborus nyblaei* fourth instar larvae, number of anal fan setae does significantly differ. I have therefore interpreted the large number of anal fan setae as autapomorphic for *Chaoborus nyblaei*.

The egg structure and type of egg mass of *Chaoborus trivittatus* is extremely similar to those of species of *Chaoborus sensu stricto*. Because *Chaoborus sensu stricto* is the sister group of *Schadonophasma* it is probable that the condition found in *Chaoborus trivittatus* represents the plesiomorphic state within *Schadonophasma*. However, it is possible that the character state of *Chaoborus trivittatus* represents a convergence with species of *Chaoborus sensu stricto*. A 'layer of jelly-like substance' or 'thin gelatinous sheath' around individual eggs (= thick exochorion?) of some species has been described (MacDonald, 1956; McGowan, 1976; Sikorowa, 1973) and, if these features are homologous with those of *Chaoborus cooki* and *Chaoborus nyblaei*, they might be considered plesiomorphic within *Schadonophasma*. However, the eggs of these other species of *Chaoborus* need to be better studied before such inferences can be made.

The proposed phylogeny of the species of *Schadonophasma* is given in Figure 38.

Zoogeography and speciation events

Hennig (1966b) has shown that zoogeographic inferences are dependent upon accurate interpretation of the evolutionary relationships of organisms. Because it seems likely that detailed study of *Chaoborus* species, both extant and fossil, will alter the phylogeny of *Chaoborus* as proposed here, I will not discuss the zoogeography of the genus. However, the inferred sister group relationship between

Schadonophasma and *Chaoborus sensu stricto* is probably correct.

Because all extant species of *Schadonophasma* and *Chaoborus sensu stricto* are found only in north temperate regions it would be reasonable to assume that the ancestor which gave rise to extant species of *Schadonophasma* was present in the north temperate region. Distributions of species of *Chaoborus sensu stricto* give no clues as to where specifically this ancestor may have arisen.

In the following discussion of the speciation event giving rise to *Chaoborus cooki* and *Chaoborus nyblaei*, I have assumed that *Chaoborus nyblaei* has had or does have a continuous Palaearctic distribution. However, future work may indicate that *Chaoborus nyblaei* has been, and is presently, restricted to Fennoscandia. A more likely explanation of the speciation event giving rise to *Chaoborus cooki* and *Chaoborus nyblaei* would suggest that dispersal of adults (or possibly desiccation resistant eggs on the feet of migrating shorebirds) took place over the North Atlantic during a period of climatic amelioration.

There are two equally probable zoogeographic interpretations of the history of *Schadonophasma* species (Figure 39).

The first suggests that the ancestor of extant *Schadonophasma* species was Holarctic in distribution. A split of its populations into Nearctic and Palaearctic elements resulted in the lineage giving rise to *Chaoborus trivittatus* and to the ancestor of *Chaoborus cooki* and *Chaoborus nyblaei* (hereafter referred to as *Chaoborus cooki-nyblaei*). The Palaearctic species then reinvaded North America and subsequently was split into Palaearctic and Nearctic populations which gave rise to *Chaoborus nyblaei* and *Chaoborus cooki* respectively. The model only requires allopatric speciation and dispersal to have taken place. A land bridge between Asia and North America is known to have appeared and disappeared a number of times during the Tertiary and Quaternary (Hopkins, 1967, 1972) which could have provided, during certain periods, a barrier to contact between Asian and North American populations.

The second zoogeographic hypothesis suggests that the ancestor of extant *Schadonophasma* species arose in North America and speciated there to give rise to the lineages resulting in *Chaoborus trivittatus* and *Chaoborus cooki-nyblaei*. Although an allopatric speciation model might explain the speciation event in North America resulting in the lineages which gave rise to *Chaoborus trivittatus* and *Chaoborus cooki-nyblaei*, it seems most likely that the invasion into temporary waters by *Chaoborus cooki-nyblaei* was not the result of geographical isolation. Although the lineage might have invaded temporary ponds because of competition with other *Chaoborus* species as a geographic isolate, it seems more likely that, especially considering the degree to which *Chaoborus trivittatus* and other *Chaoborus* species can coexist (Stahl, 1966), this would not result in a speciation event. It is also difficult to imagine two isolated geographical areas which contained populations of the ancestral species, one of which contained only temporary waters conducive to the evolution of a temporary pond species.

The available data for *Schadonophasma* species allow for a hypothesis of sympatric speciation. The following are hypothesized events, as indicated by this study, for *Schadonophasma* species and features of species of *Chaoborus sensu stricto*.

The Nearctic species ancestral to extant *Schadonophasma* species inhabited permanent waters with fourth instar larvae as the over-wintering stage. Upon emergence of adults in spring, the males formed swarms on the periphery of the permanent water body and mated with females after these emerged. These are features of *Chaoborus trivittatus* and those species of *Chaoborus sensu stricto* for which information is available, and are therefore, probably plesiomorphic characteristics of *Schadonophasma*. As previously shown for the two species of *Chaoborus trivittatus* and *Chaoborus americanus*, which overwinter as fourth instar larvae in permanent ponds (p. 186), the dispersing females occasionally laid eggs in temporary ponds. Eggs which hatched resulted in larvae which could not survive overwintering in this habitat. This type of egg was strongly selected against, as all larvae which hatched from them in

temporary ponds would die. Tauber *et al.* (1977) have shown that mutation of a single allele can result in the appearance of diapause in individuals of a population. If this feature is controlled by a single gene in *Schadonophasma* species, crosses of male *Chaoborus trivittatus* and female *Chaoborus cooki* resulting in diapausing eggs would suggest that the allele for diapausing eggs is dominant. I have assumed this to be the situation in the following discussion. The primitive non-diapausing egg is represented by autosomal recessive alleles *aa*. Mutation resulted in the production of a dominant *Aa*, producing diapausing eggs. A female carrying these genes laid her eggs in a temporary pond, which then diapaused in this habitat. Resistance to complete desiccation might not have evolved at this stage because, at least for the temporary ponds I investigated, the bottoms were quite moist; probably, in some ponds, moist enough to prevent desiccation of eggs. Larvae which hatched out in spring from these overwintered eggs would mature to adulthood at a later time than would those in permanent ponds, which emerge as adults early in spring. This might give at least a certain degree of temporal isolation. However, as discussed above (p. 184), *Chaoborus trivittatus* might be multivoltine in certain regions and this may have provided some temporal overlap between two populations of the ancestral species.

The adults which emerged from the temporary pond would, as did the parent population in permanent ponds or lakes, have swarmed and mated at the pond periphery. This homogamic behavior led to further segregation of populations and ensured an increase in numbers of individuals carrying this gene. The resultant adults would carry the alleles *AA* or *Aa*. Any *aa* eggs laid in temporary ponds would be eliminated as larvae. *AA* or *Aa* eggs subsequently laid in permanent ponds would survive and hatch in the spring as first instars, but any other *Chaoborus* larvae, if present, would be fourth instar and these first instars would probably be cannibalized. To hypothesize the removal of heterozygotes from the temporary pond lineage (and therefore the continued production of *aa*), I suggest that the allele *A* became associated with co-dominant or recessive features conducive to temporary pond existence and therefore, as the temporary pond populations adapted to the temporary pond environment, heterozygotes were selected against. Adult behavior and comparatively reduced ovarian development of extant *Chaoborus cooki*, may be examples of such adaptations, but these also may have evolved after the speciation had occurred.

Through temporal disjunction of mating periods, homogamic mating, complete selection against overwintering larvae in temporary ponds, and partial selection against heterozygotes in temporary ponds and overwintering eggs in permanent ponds, the two lineages giving rise to *Chaoborus trivittatus* and *Chaoborus cooki-nyblaei* became genetically isolated. These suggested events are summarized in Figure 40.

Chaoborus cooki-nyblaei invaded the Palaearctic region, and subsequent barriers to reproduction, as described for the first zoogeographic hypothesis, resulted in isolated populations which gave rise to *Chaoborus cooki* and *Chaoborus nyblaei*.

The sympatric speciation model is dependent at least on the assumption that *Chaoborus nyblaei* does in fact overwinter as an egg. Although this was inferred from available data, I have no direct evidence that this is so. Study of the life cycle of *Chaoborus nyblaei* would therefore provide a test of this hypothesis. If study of the populations I have described as 'populations *incertae sedis*' show these to be one or more species, this may provide additional evidence for testing this proposal of sympatric speciation.

CONCLUDING REMARKS

On the basis of their work, taxonomists should indicate particularly fruitful areas for future research: those concerned primarily with the group studied in particular, and those concerned with systematic problems in general.

Because of the paucity of museum material of specimens of *Schadonophasma*, future endeavors relating to the systematics of the subgenus must await further collecting. Some details concerning the bionomics of species may bear further investigation, as indicated in the text. In particular, investigation of the life cycle of *Chaoborus nyblaei* and the specific affinities of the 'populations *incertae sedis*' may provide additional insights into the systematics of species of *Schadonophasma*. The phyletic relationships of species of *Chaoborus* are yet poorly known. Fossil species and extant species from the tropics, are particularly in need of study and the entire genus is worthy of a complete revision.

In general, this study suggests that investigation of the bionomics of species of some groups may provide additional tests of the sympatric speciation model. Because of domination of evolutionary concepts by the allopatric speciation model, the full implications and requirements of the sympatric speciation model are poorly understood. These aspects of the model can only become clear when additional information on bionomics of organisms which may have speciated sympatrically become available.

As is well illustrated by the work of Bush (1975b) on tephritid fruit flies, a sympatric speciation model can only be justifiably invoked from a solid base of bionomic data. Although allopatric speciation has in the past been the favored hypothesis to explain differentiation of organisms, it is also evident that only morphological and distributional data are available for most organisms. Therefore, until adequate bionomic data are available for a large array of taxonomic groups, it will be difficult to estimate the frequency of occurrence of sympatric speciation. As discussed by Bush (1975a), sympatric speciation occurs under special genetic and environmental conditions. It seems clear that, in certain groups (mammals, birds, and carabid beetles), such conditions are rarely, if ever met. In the genus *Chaoborus*, considering the similarity of the life cycle of most species, it appears that sympatric speciation occurs with less frequency than does allopatric speciation. Nevertheless, some groups, like some species groups of tephritid flies, appear to be more prone to speciate sympatrically. This pattern suggests, therefore, that systematists should not apply the *most common* mode of speciation to all taxonomic groups under investigation. Rather, each speciation model should be based on data available for that group.

An aspect not explicitly clear in previous discussions of sympatric speciation concerns the phyletic relationships and zoogeography of the organisms concerned — essential considerations in any speciation model. This study of *Schadonophasma* provides an example of how zoogeographic considerations may provide additional evidence for elucidation of sympatric speciation.

In conclusion, it is the intensive study of only a few closely related species, as here reported for the subgenus *Schadonophasma*, which can most fruitfully provide the basic information necessary to test hypotheses of sympatric speciation.

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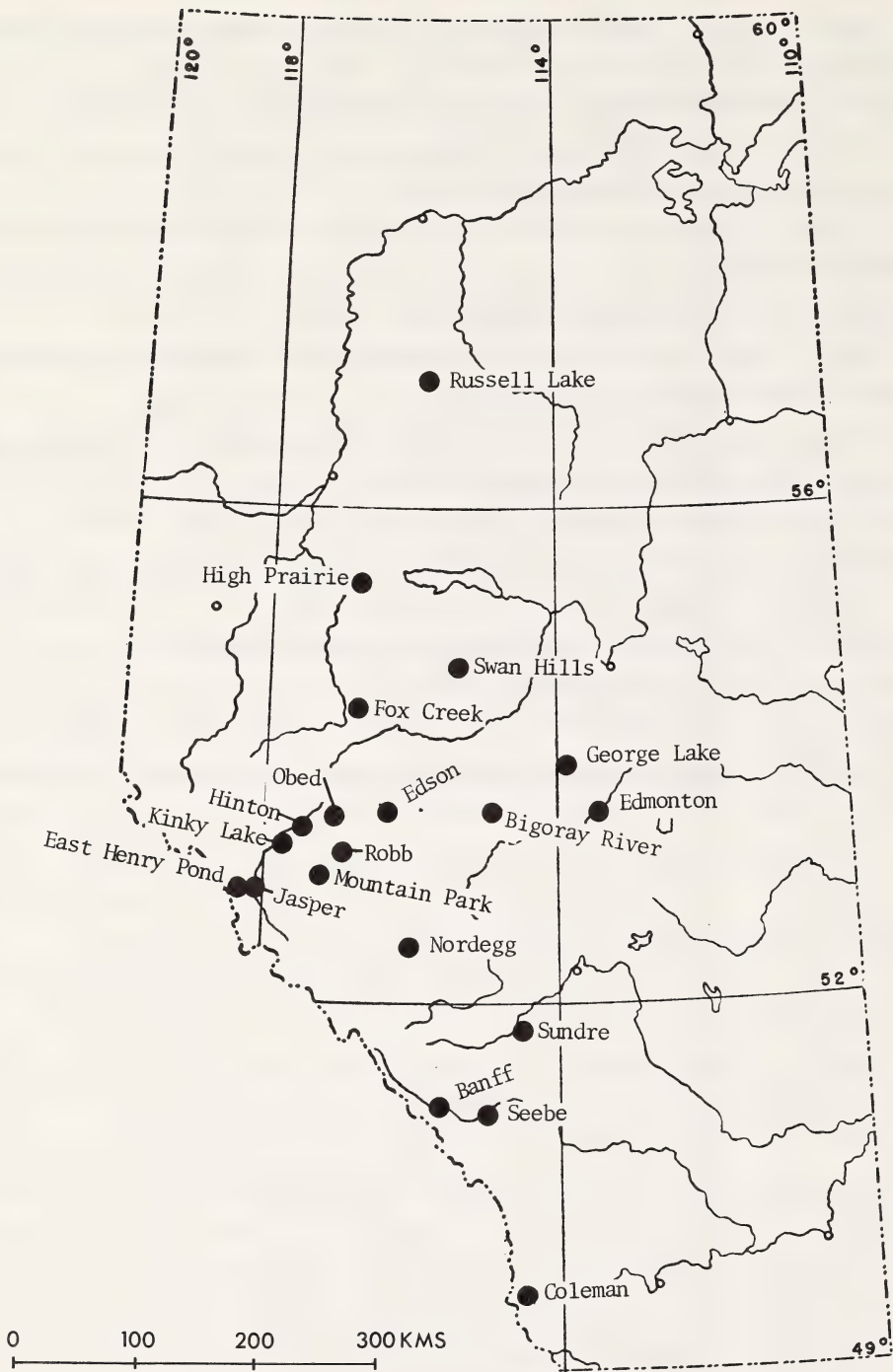


Figure 1. Place names in Alberta cited in text.

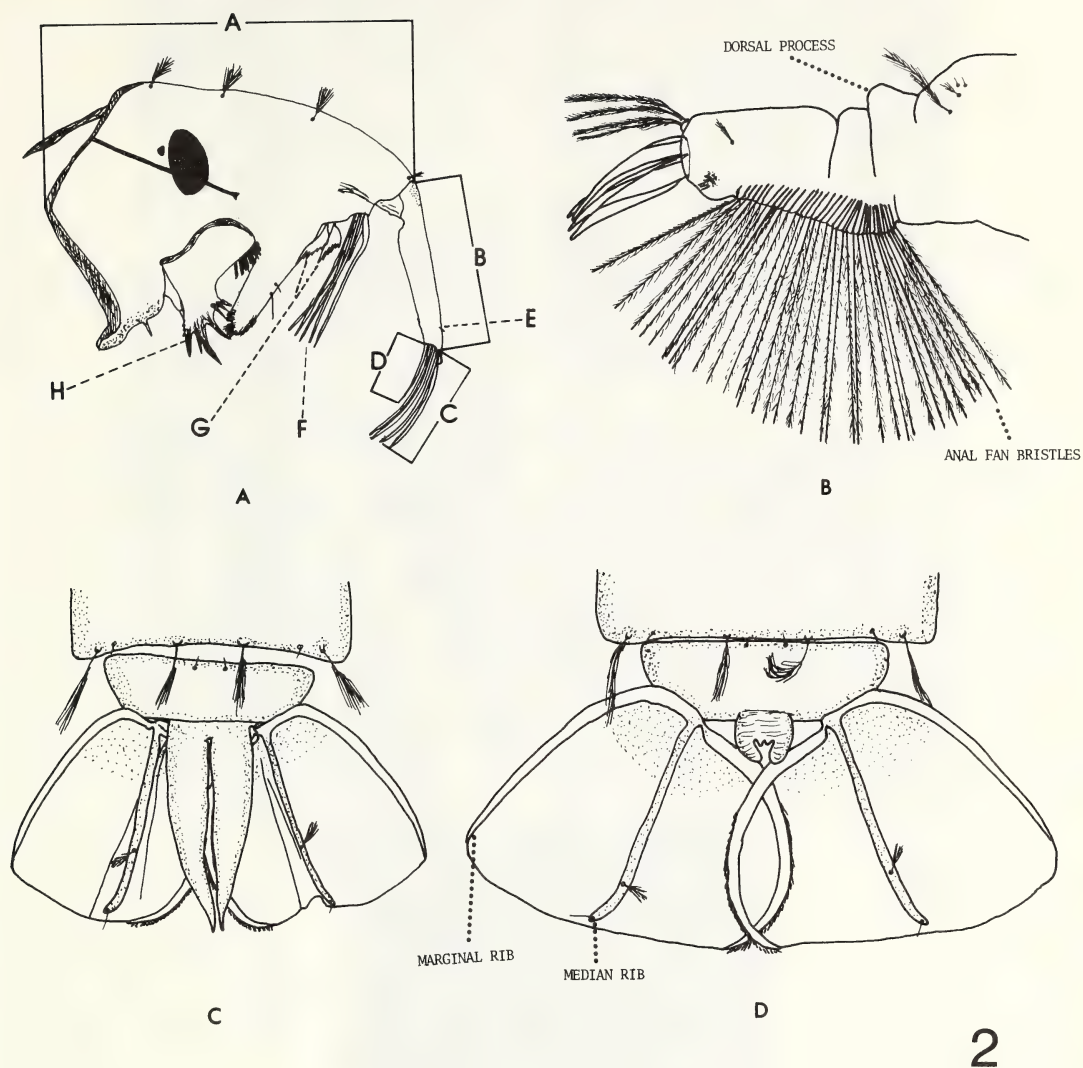


Figure 2. A. Characters and measurements of head capsule of fourth instar larva: A. Head capsule length; B. Antennal length; C. Long antennal blade length; D. Short antennal blade length; E. Antennal seta; F. Postantennal filaments; G. Prelabral appendages; H. Mandible; total length of mandibular fan bristles and labral brush setae is not shown; B. Characters of terminal abdominal segments of fourth instar larva. C. Terminalia of male pupa. D. Terminalia of female pupa. All drawings from specimens of *Chaoborus cooki*.

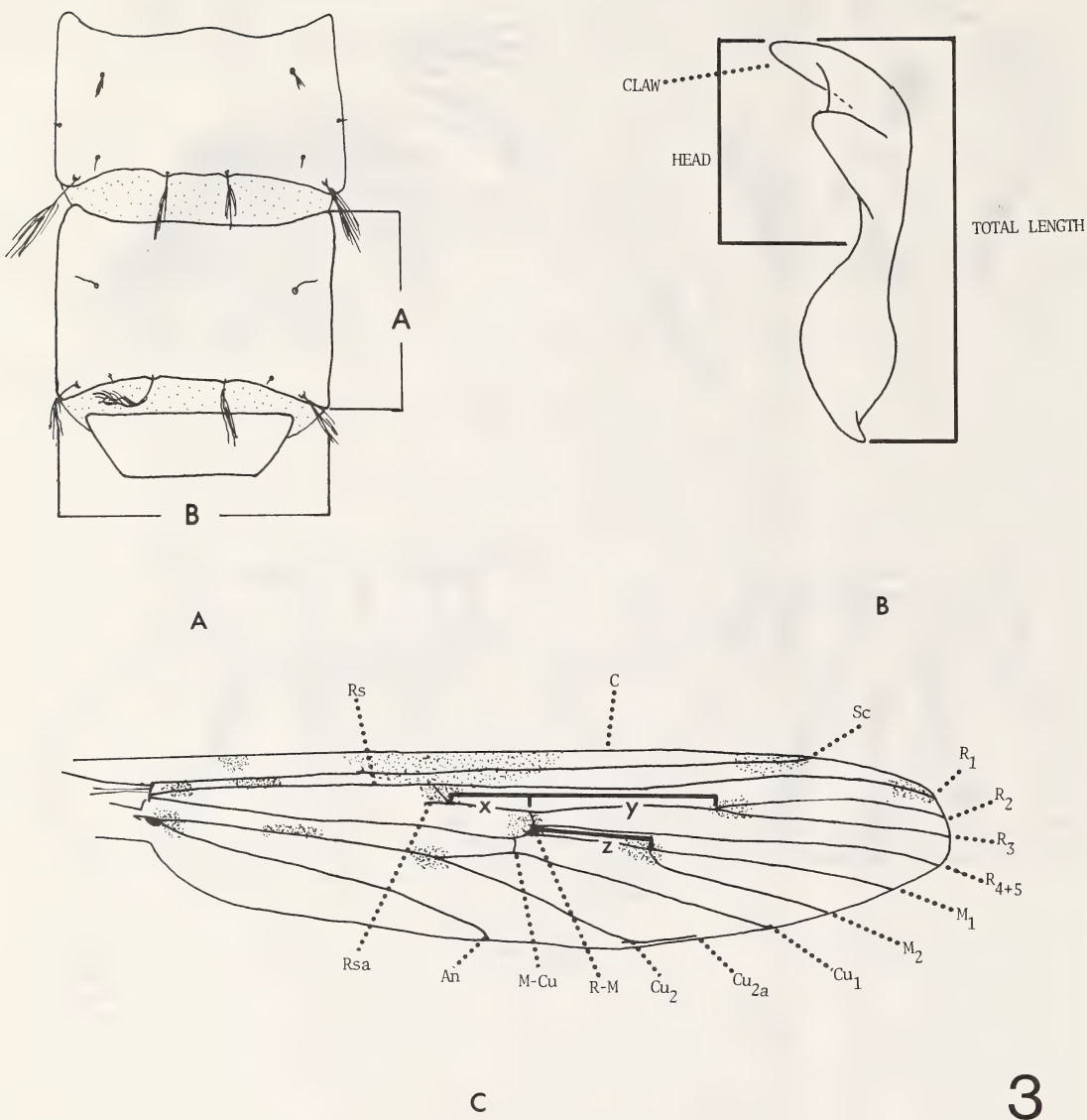
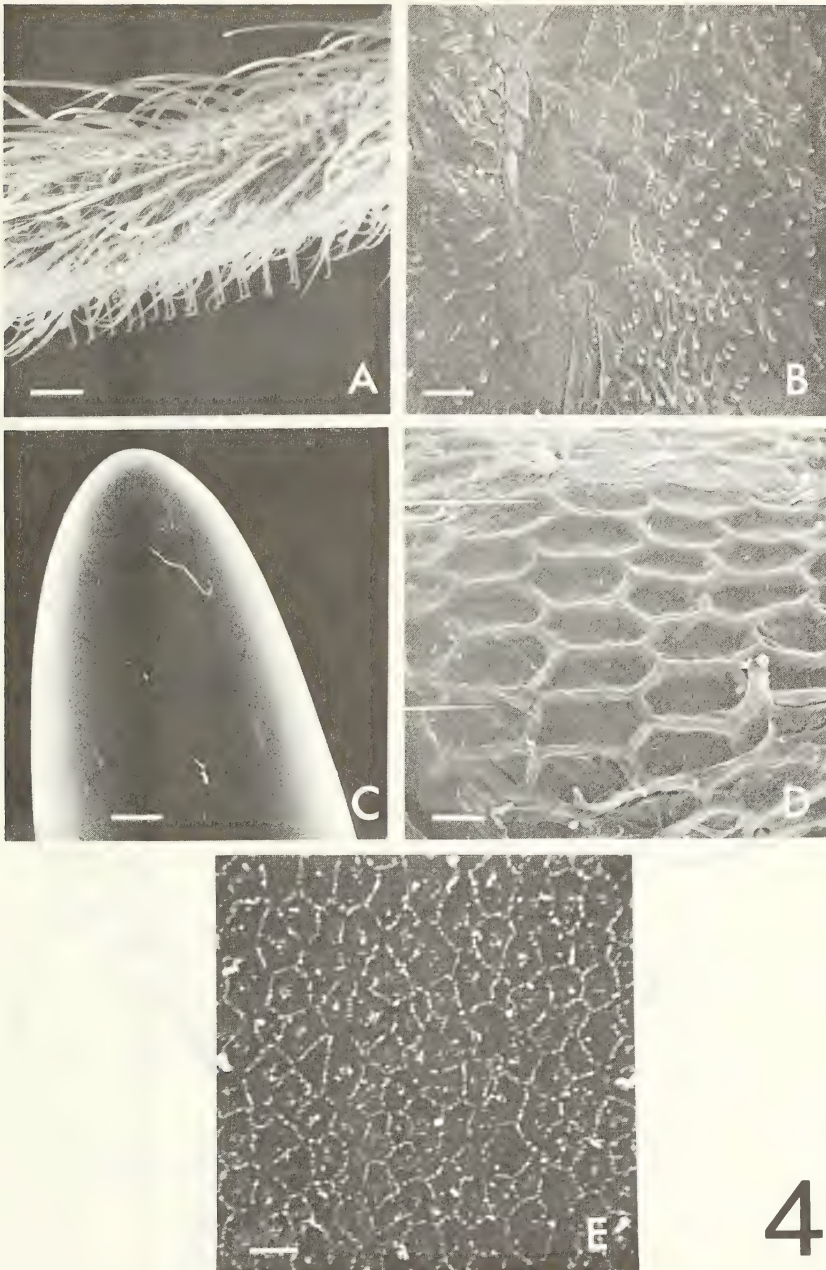
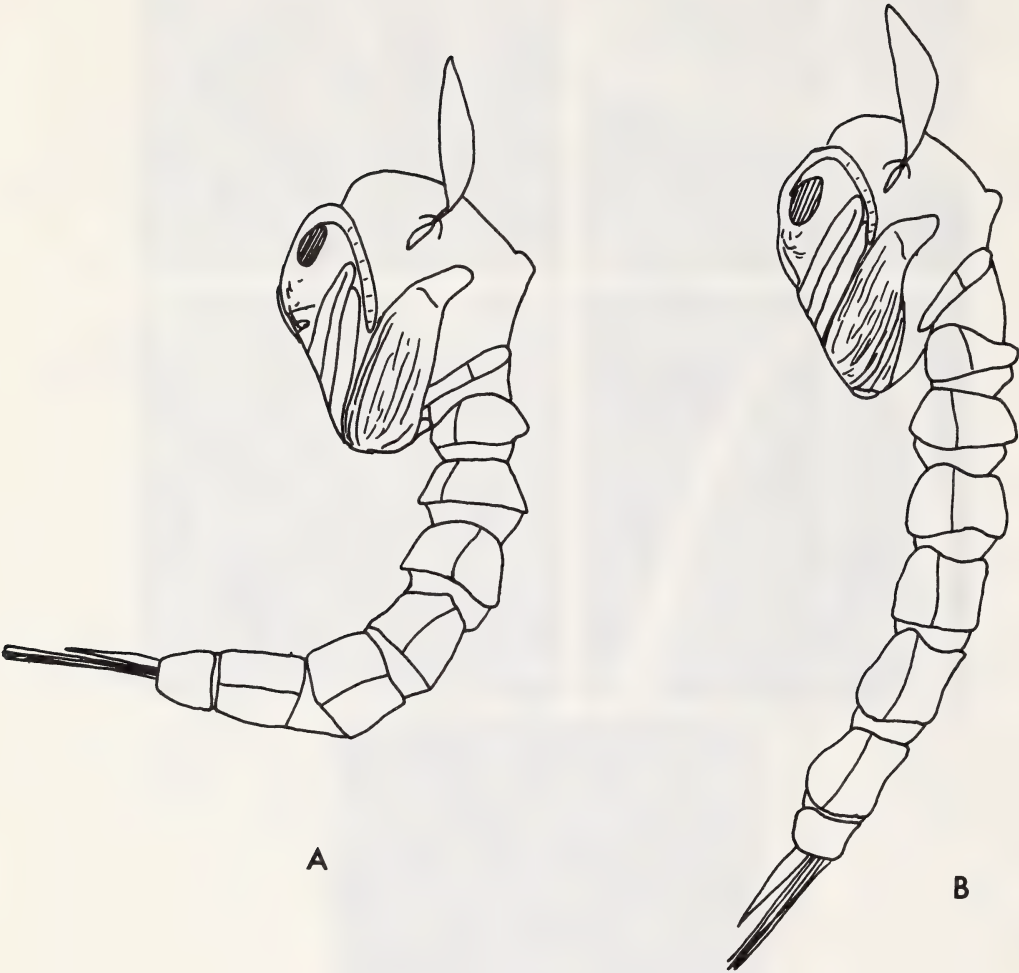


Figure 3. Terms and measurements - A. Terminal abdominal segments of pupa: A. Length of abdominal segment VII; B. Width of abdominal segment VII. B. Male adult penis valve. C. Wing of adult (male).



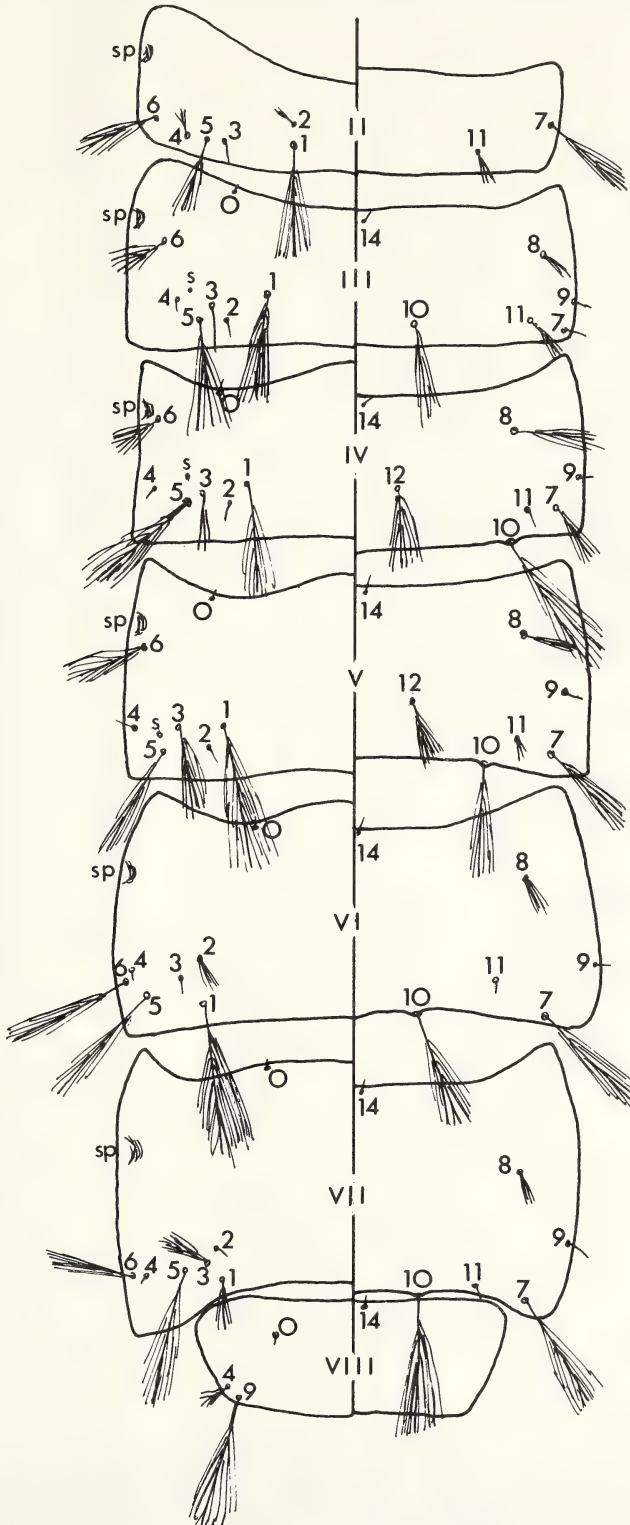
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Figure 4. Scale line = 20 μm for Figures A-D and 1 μm for Figure E. A. Third tarsomere of midleg of female adult. B. Microsculpture of dorsal margin of head capsule of fourth instar larva. C. Exochorion of egg of *Chaoborus trivittatus*. D. Exochorion of egg of *Chaoborus cooki*. E. Sculpturing of dorsum of exochorion of *Chaoborus trivittatus*.



5

Figure 5. Posture of live pupae. A. *Chaoborus cooki*. B. *Chaoborus trivittatus*. Drawings from photographs of live pupae.



6

Figure 6. Abdominal chaetotaxy of pupa of *Schadonophasma*. Setae numbered after Belkin *et al.* (1970). S: sensilla; sp: spiracular scar.



7

Figure 7. Scale line = 0.1 mm. Antenna and dorsal outline of head capsule of larval instars of *Schadonophasma*. Antennae: A. First instar; B. Second instar; C. Third instar; D. Fourth instar. Dorsal outline of head capsule: E. First instar of *Chaoborus cooki*; F. First instar of *Chaoborus trivittatus*; G. Second instar; H. Third instar; I. Fourth instar. J. Egg burster of first instar of *Chaoborus cooki*. K. Egg burster of first instar of *Chaoborus trivittatus*.

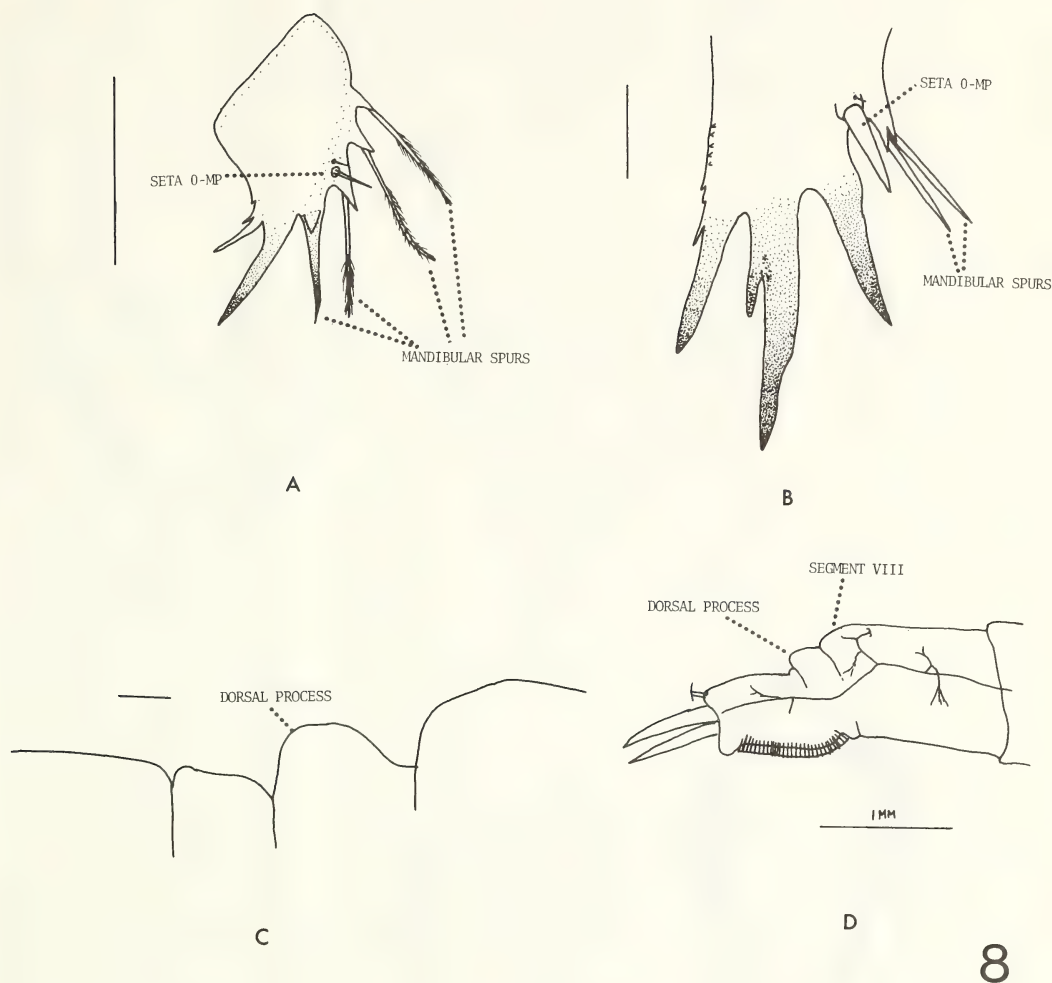


Figure 8. Except where indicated, scale line = 0.1 mm. A. Mandible of first instar larva. B. Mandible of fourth instar larva (mandibular fan not shown). C. Dorsal process of fourth instar larva of *Chaoborus nyblaei*. D. Terminal abdominal segment of fourth instar larva of *Chaoborus cooki* showing position of tracheae.

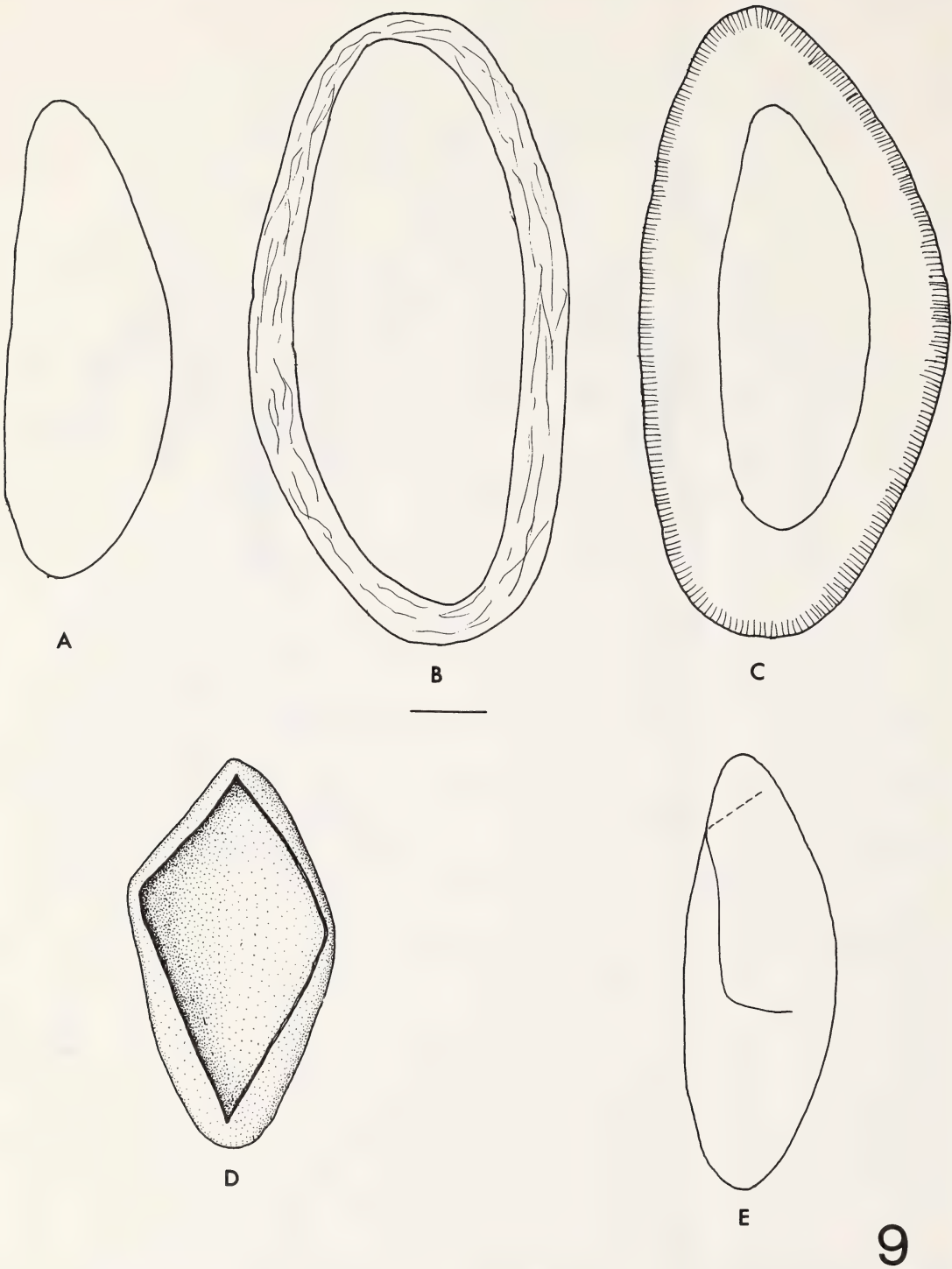


Figure 9. Scale line = 0.1 mm. Egg structure. A. *Chaoborus trivittatus*. B. *Chaoborus nyblaei*. C. *Chaoborus cooki*. Egg shell. D. *Chaoborus trivittatus*. E. *Chaoborus cooki* (fracture line indicated).

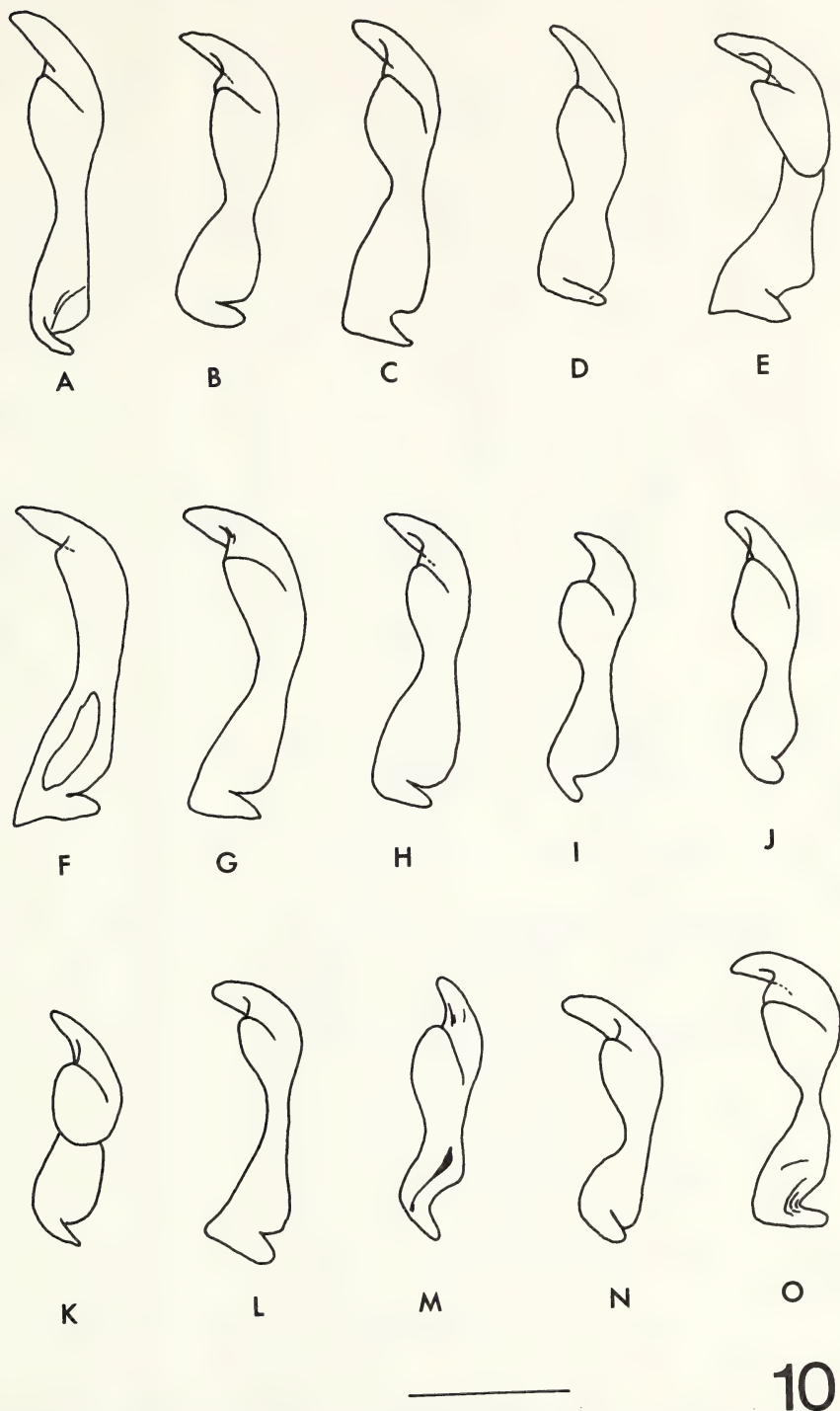


Figure 10. Scale line = 0.1 mm. Penis valves of adult male *Chaoborus trivittatus*. A–G. Intrapopulational variation of specimens from 2.4 km west of Edmonton, Alberta. H–O. Interpopulational variation of specimens from: H. Banff, Alberta; I. Hoodsport, Washington; J. North Burgess Twp., Ontario; K. Whitehorse, Yukon Territory; L. Old Chelsea, Quebec; M. Lake 241, Kenora, Ontario (holotype of *Chaoborus brunskilli*); N. Stanford, California; O. Maine (holotype of *Chaoborus trivittatus*).

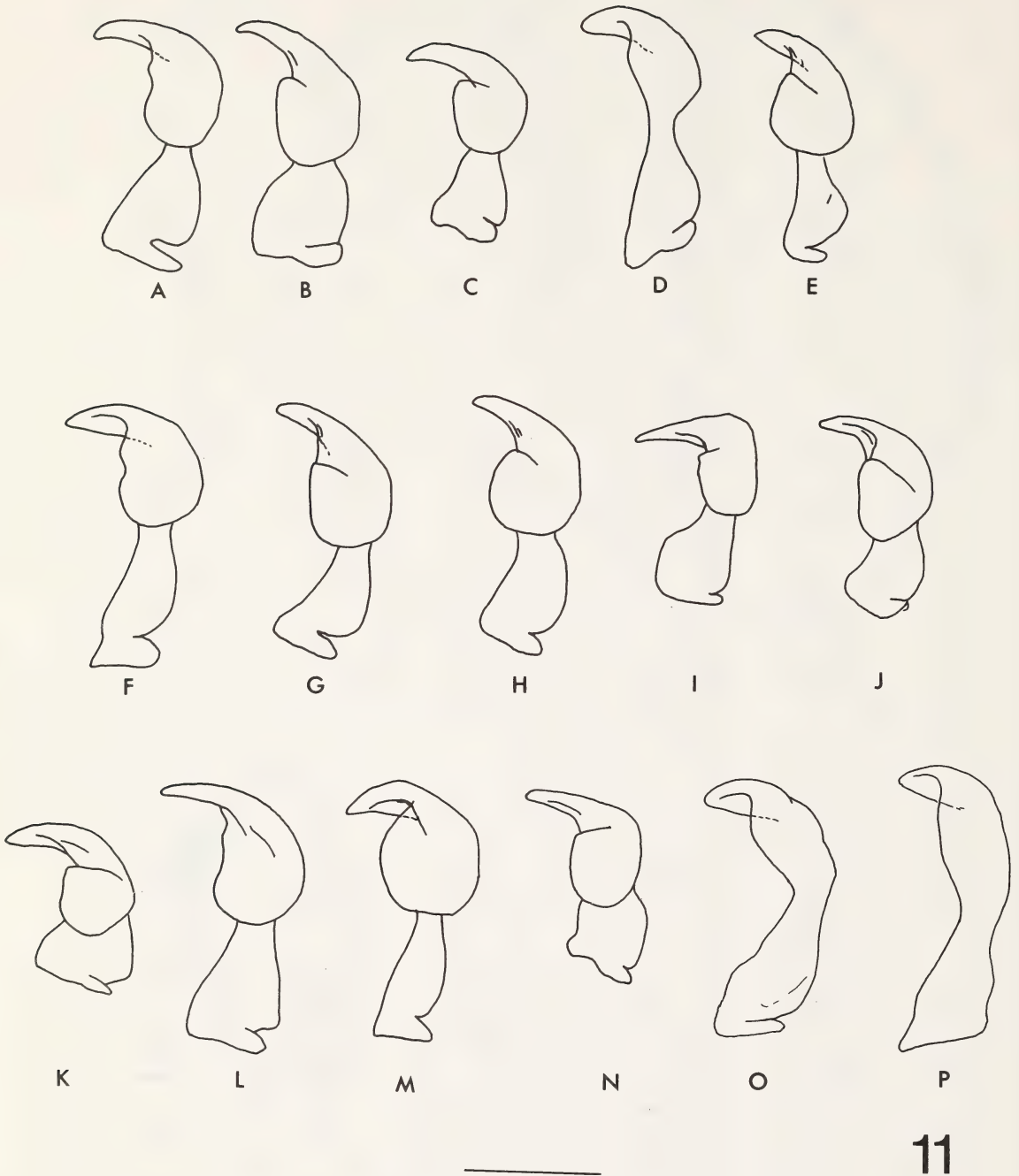


Figure 11. Scale line = 0.1 mm. Penis valves of adult male *Chaoborus cooki*. A-H. Intrapopulational variation of specimens from 1.4 km west of George Lake, Alberta. I-N. Interpopulational variation of specimens from: I. Km. 140, Dempster Highway, Yukon Territory; J. Churchill, Manitoba; K. Gillam, Manitoba; L. Whitehorse, Yukon Territory; M. Yellowknife, Northwest Territories; N. Chisholm, Ontario. Penis valves of adult male *Chaoborus nyblaei*. Specimens from: O. 2-3 km SW Nuorgam, Finland; P. Abisko, Sweden.

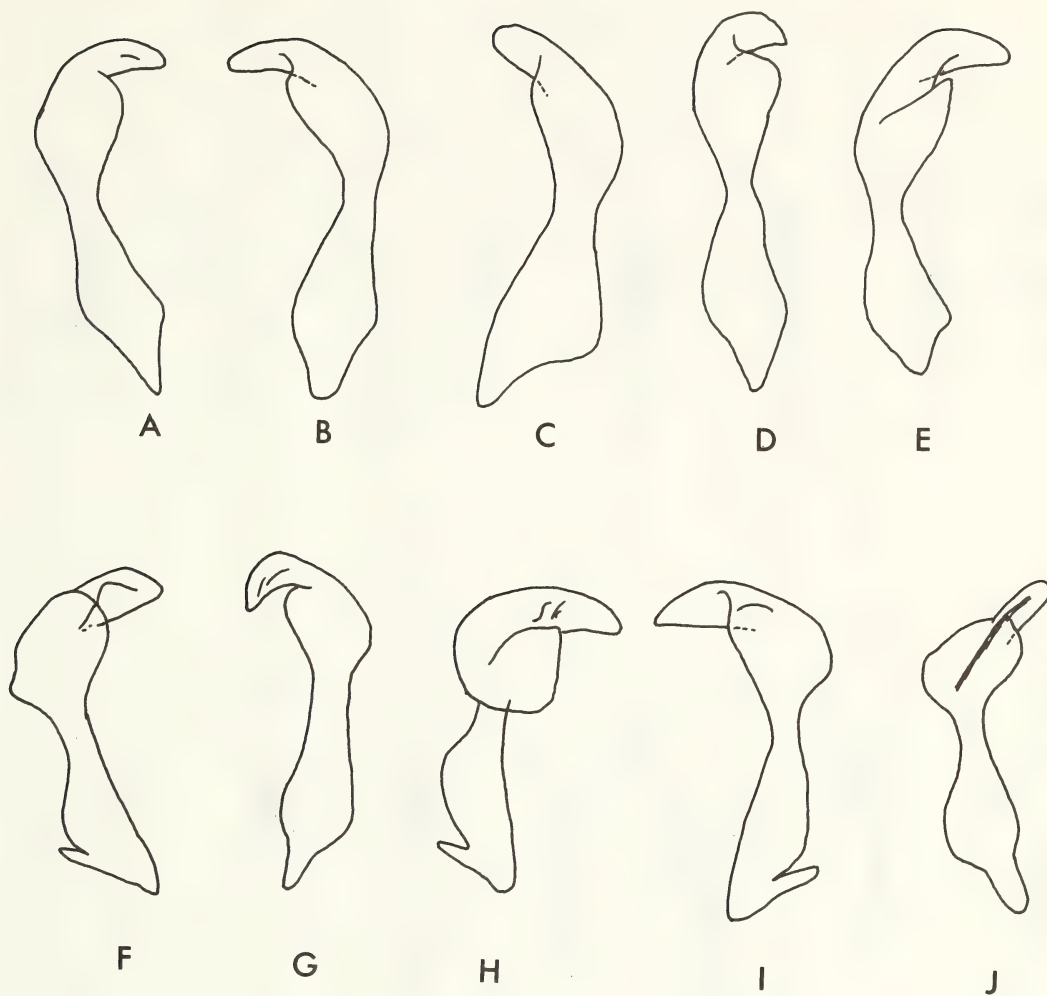
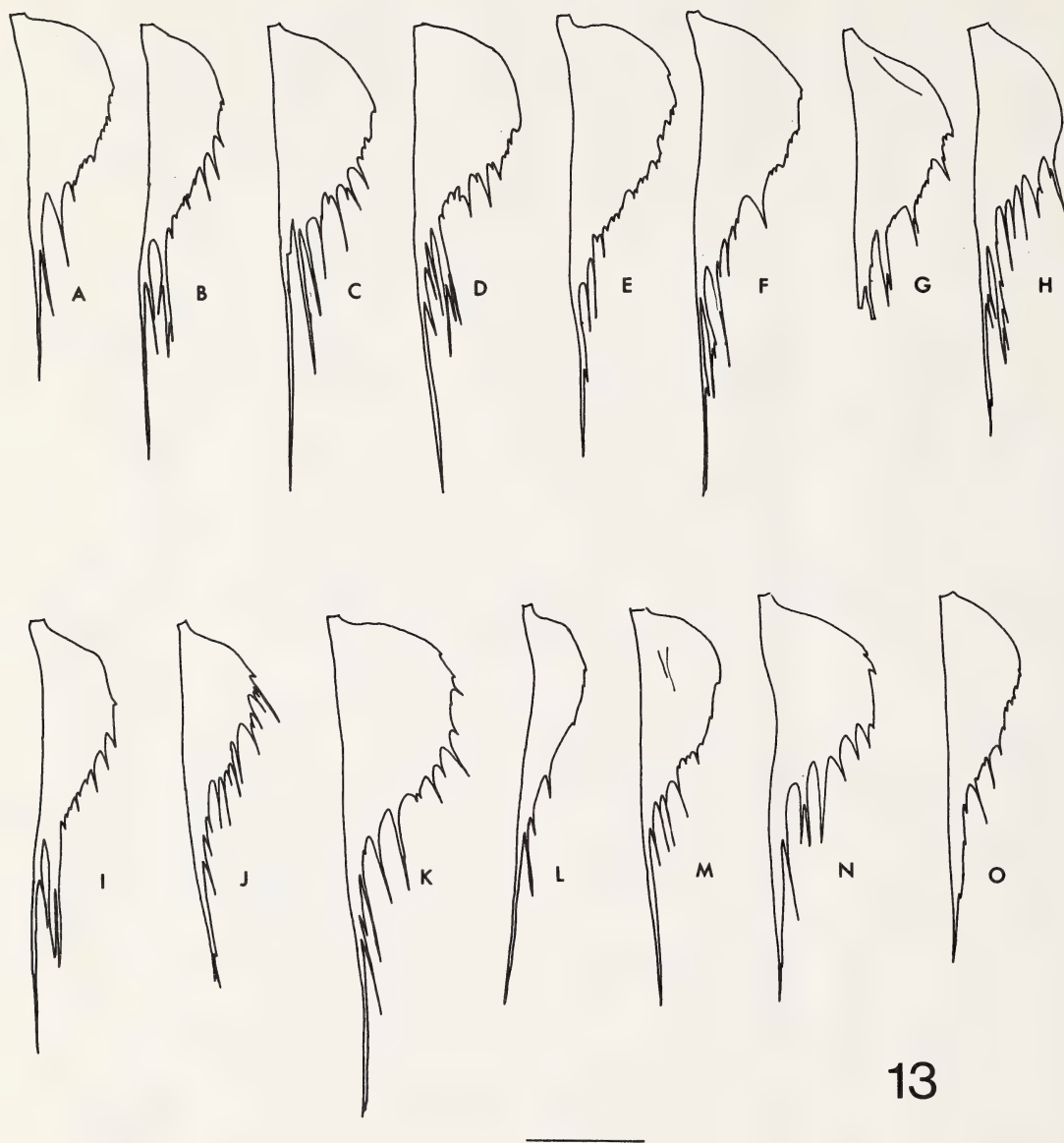


Figure 12. Scale line = 0.1 mm. Variation of penis valves of adult males due to orientation. A-E. *Chaoborus trivittatus* from 2.4 km west of Edmonton, Alberta. F-J. *Chaoborus cooki* from 32 km west of Edson, Alberta.



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Figure 13. Scale line = 0.1 mm. Prelabral appendages of fourth instar larvae of *Chaoborus trivittatus*. A–G. Intrapopulational variation of specimens from 2.4 km west of Edmonton, Alberta. H–O. Interpopulational variation of specimens from: H. 4.8 km north of St. John's, Newfoundland; I. 2.4 km west of Edmonton, Alberta; J. 2.4 km south of Robb, Alberta; K. Gwendoline Lake, British Columbia; L. 4.8 km east of Sicamous, British Columbia; M. 45 km east of Jasper, Alberta; N. Lake 241, Kenora, Ontario; O. East Henry Pond, Jasper National Park, Alberta.

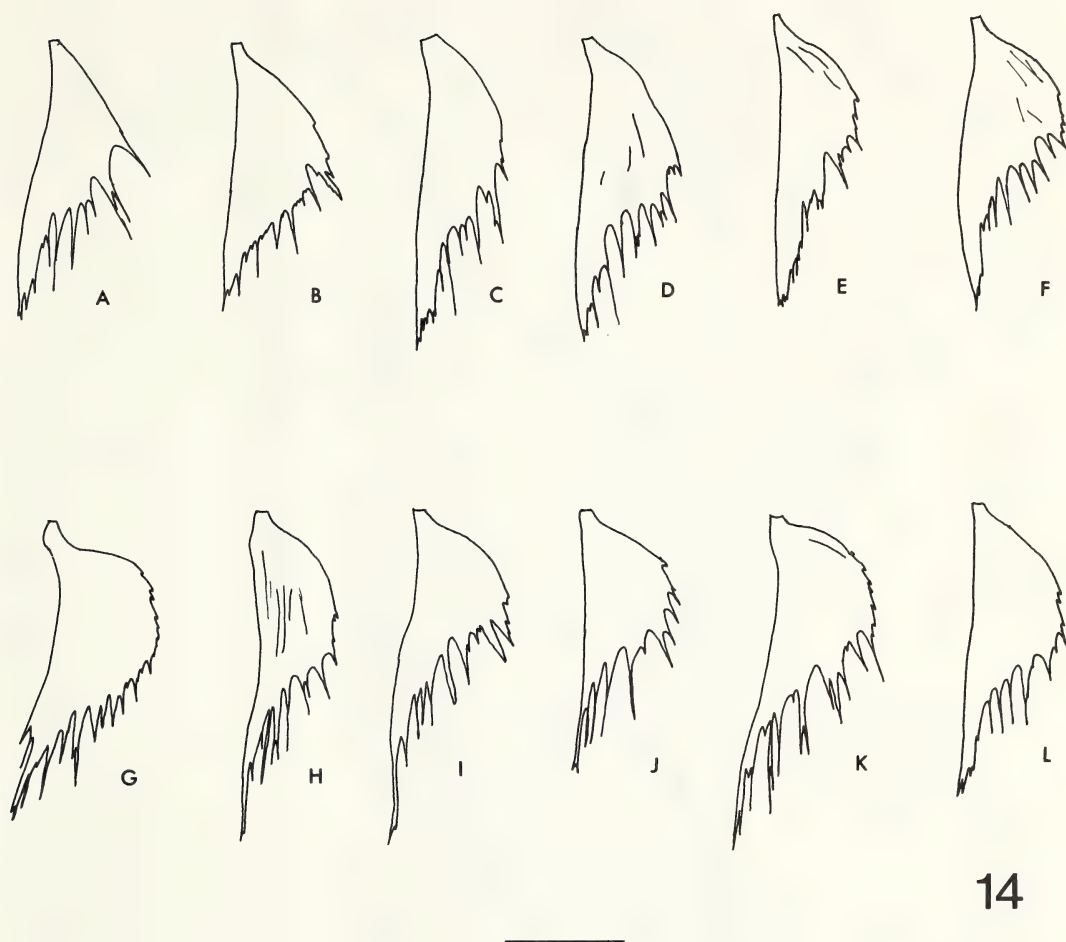
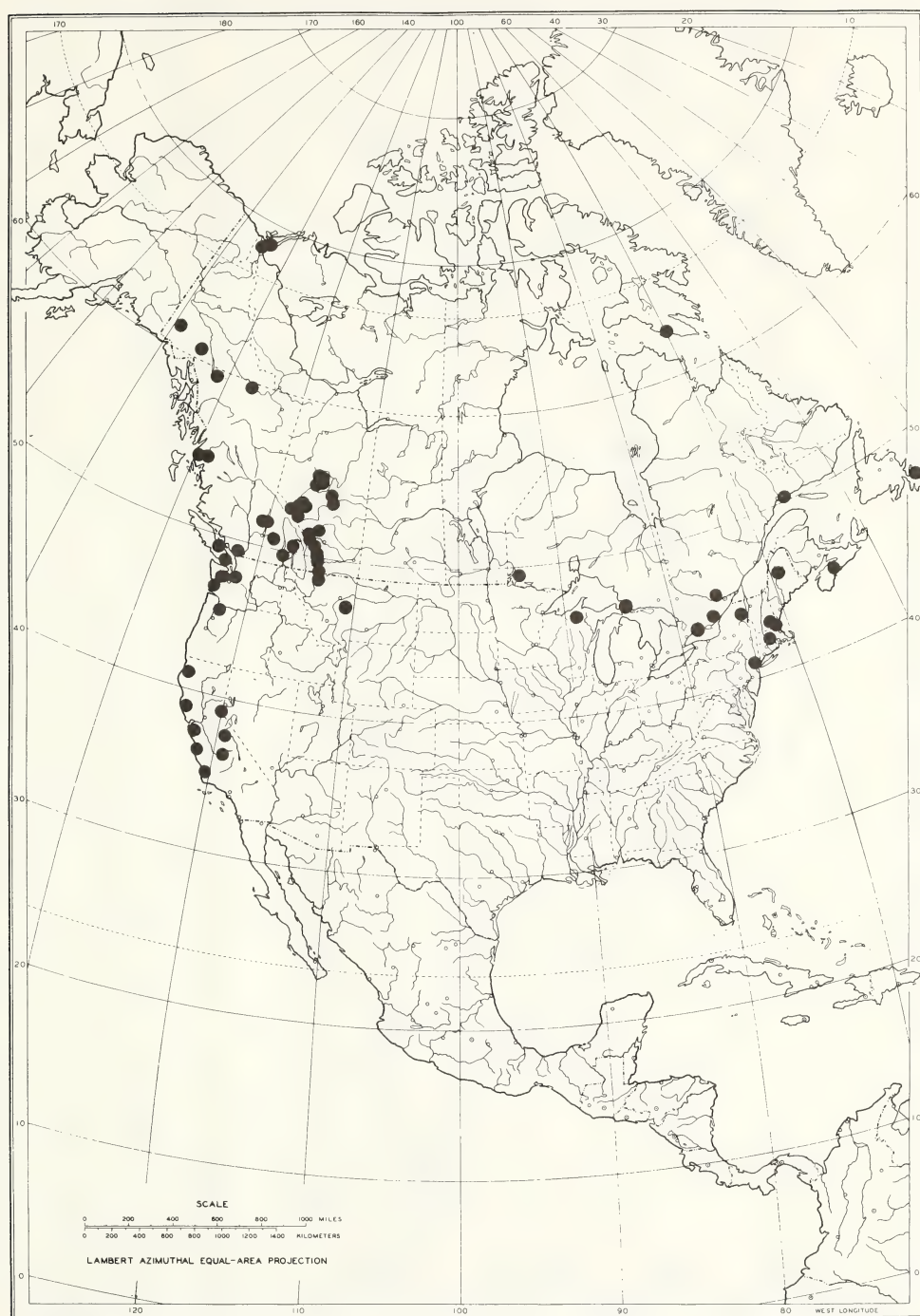


Figure 14. Scale line = 0.1 mm. Prelabral appendages of fourth instar larvae of *Chaoborus cooki*. A-F. Intrapopulational variation of specimens from 1.6 km south of Jasper, Alberta. G-L. Interpopulational variation of specimens from: G. Churchill, Manitoba; H. Pond nr. Harris River, Northwest Territories; I. Dempster Highway, Yukon Territory; J. 1.4 km west of George Lake, Alberta; K. Klutlan Glacier moraine, Yukon Territory; L. 23.3 km west of Jasper, Alberta.



Figure 15. Scale line = 0.1 mm. Prelabral appendages of fourth instar larvae of *Chaoborus nyblaei* from 2-3 km southwest of Nuorgam, Finland.



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Figure 16. Known distribution of *Chaoborus trivittatus*.

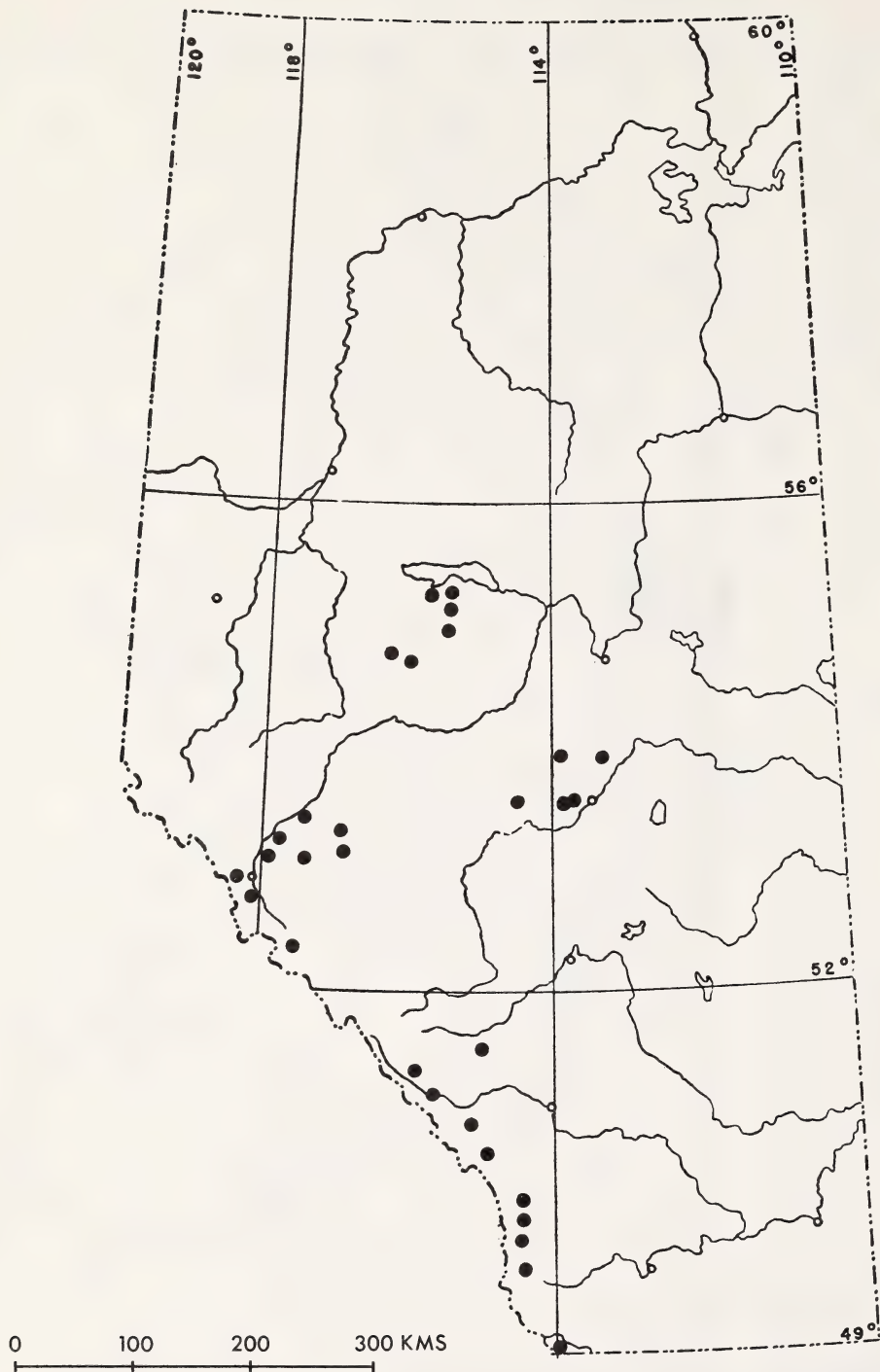
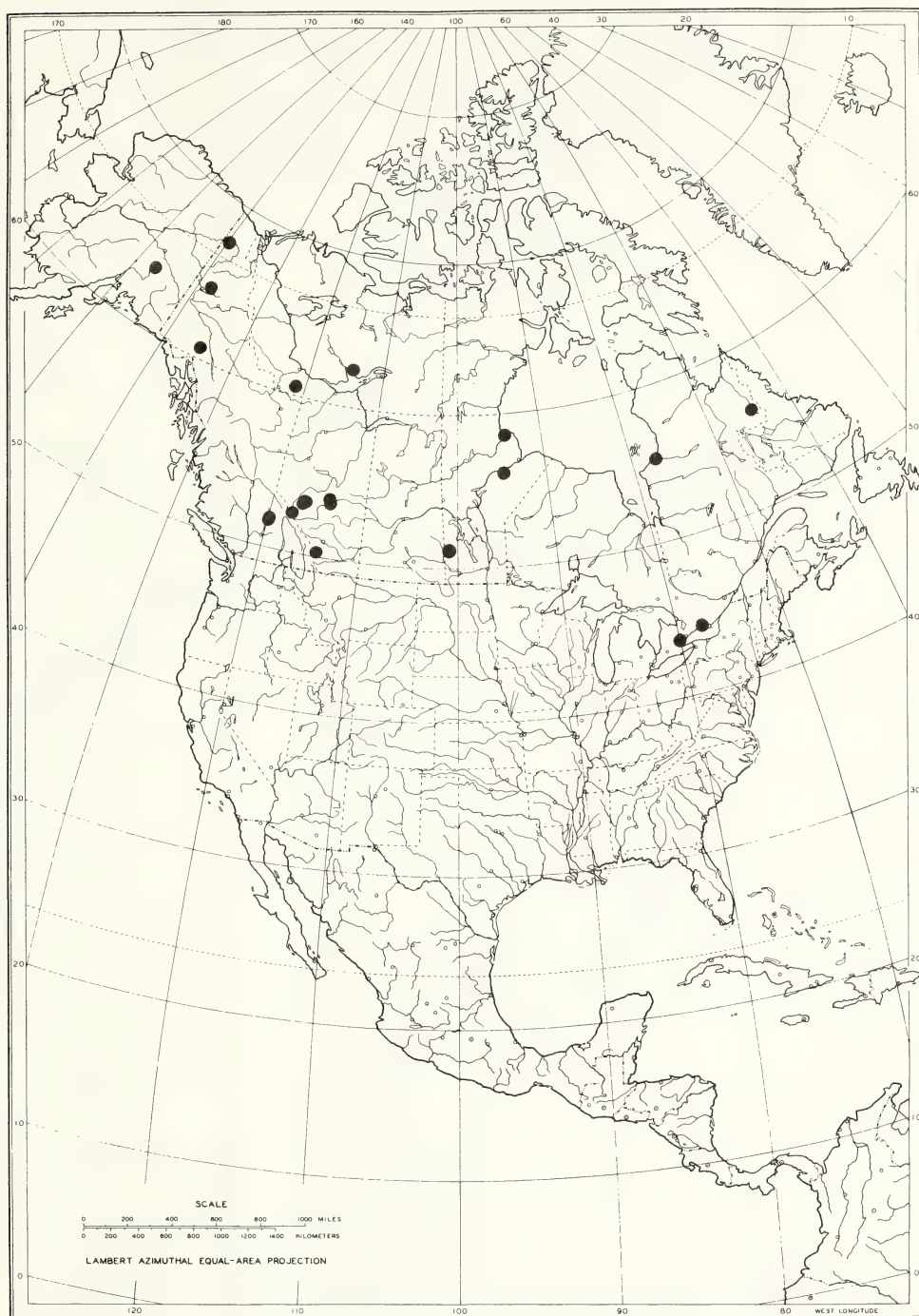


Figure 17. Known distribution of *Chaoborus trivittatus* in Alberta.



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Figure 18. Known distribution of *Chaoborus cooki*.

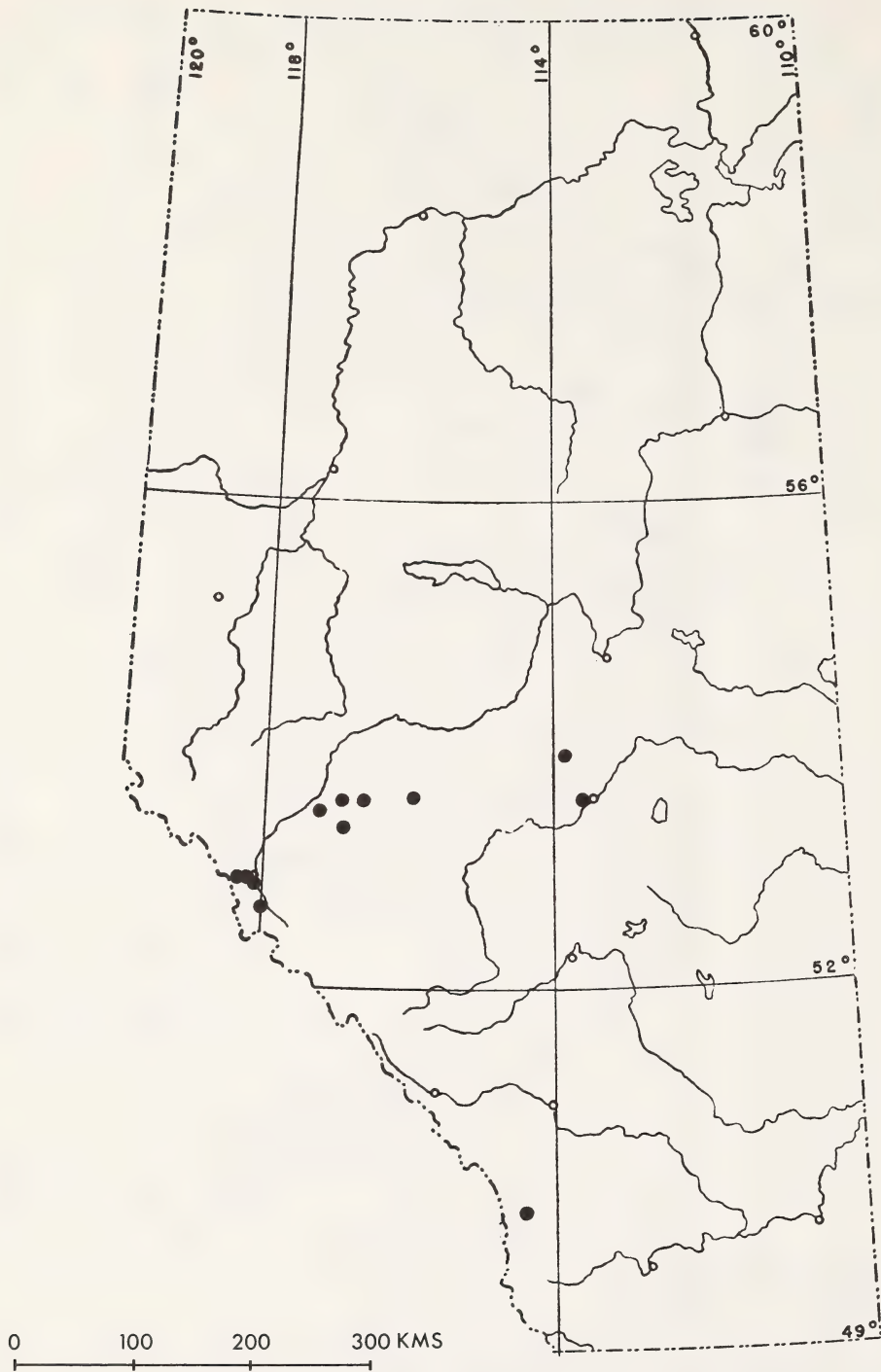


Figure 19. Known distribution of *Chaoborus cooki* in Alberta.

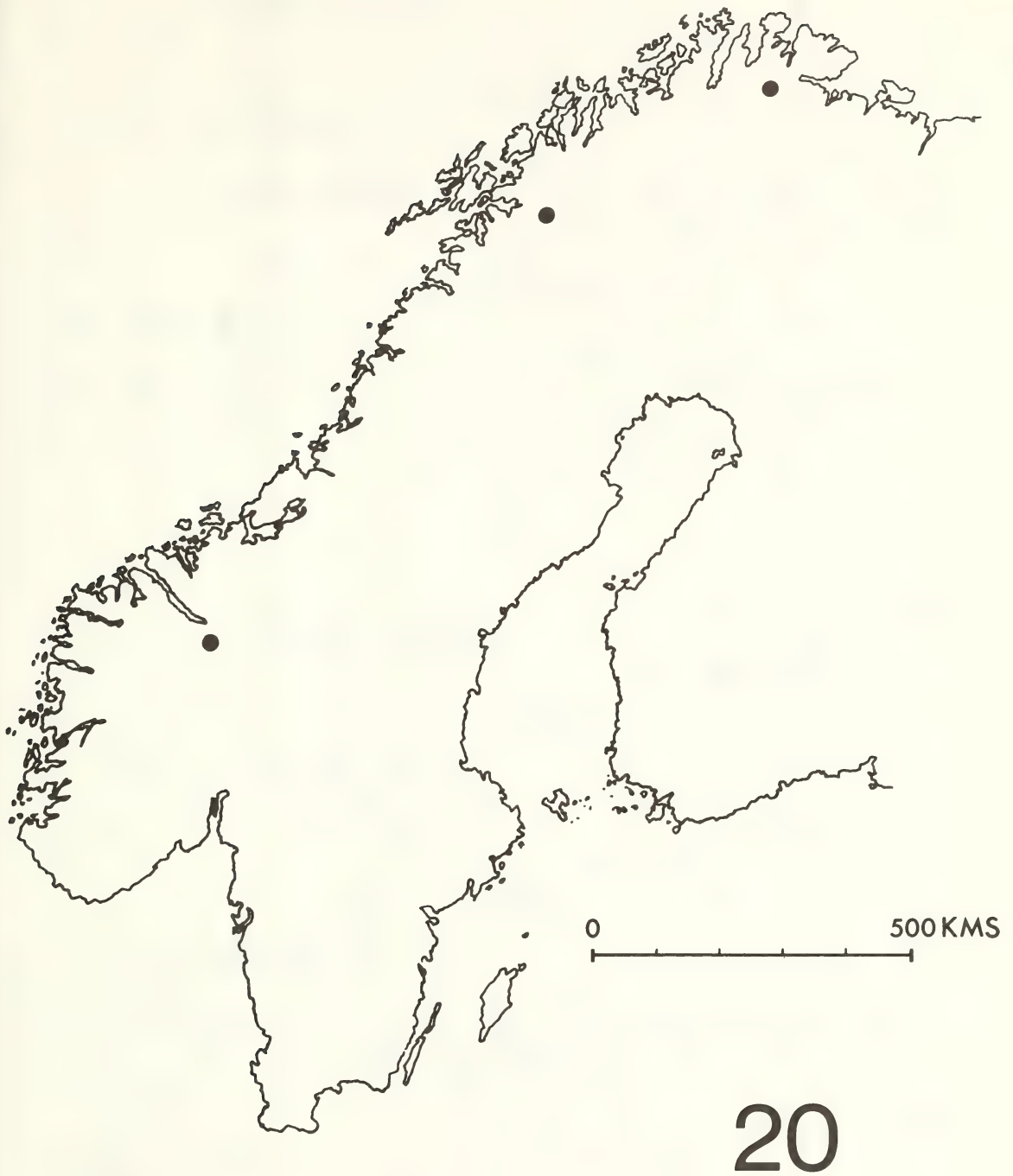


Figure 20. Known distribution of *Chaoborus nyblaei*.

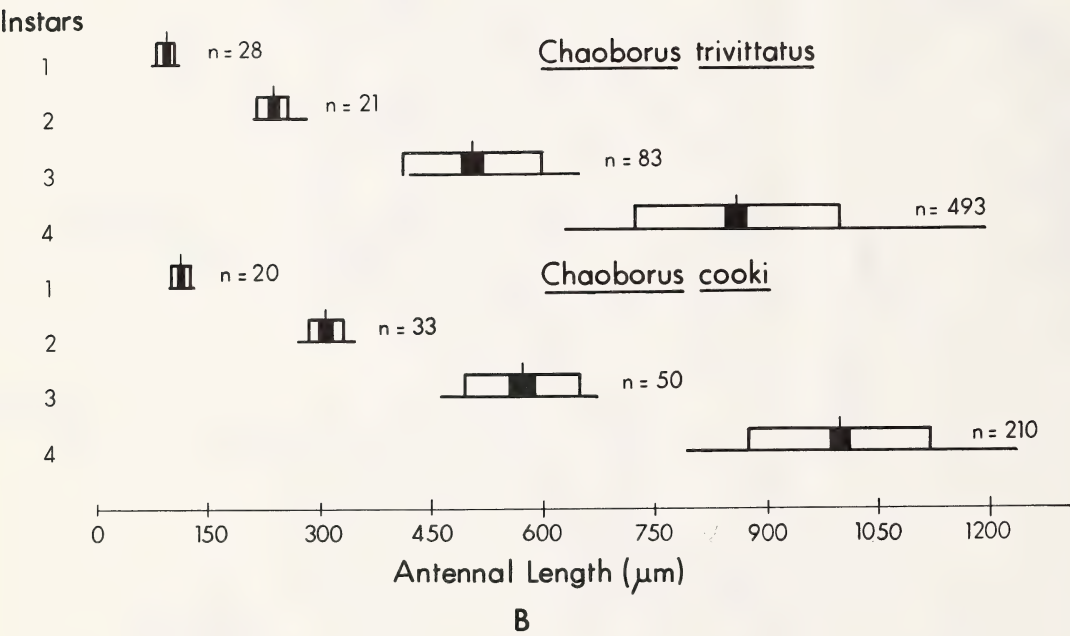
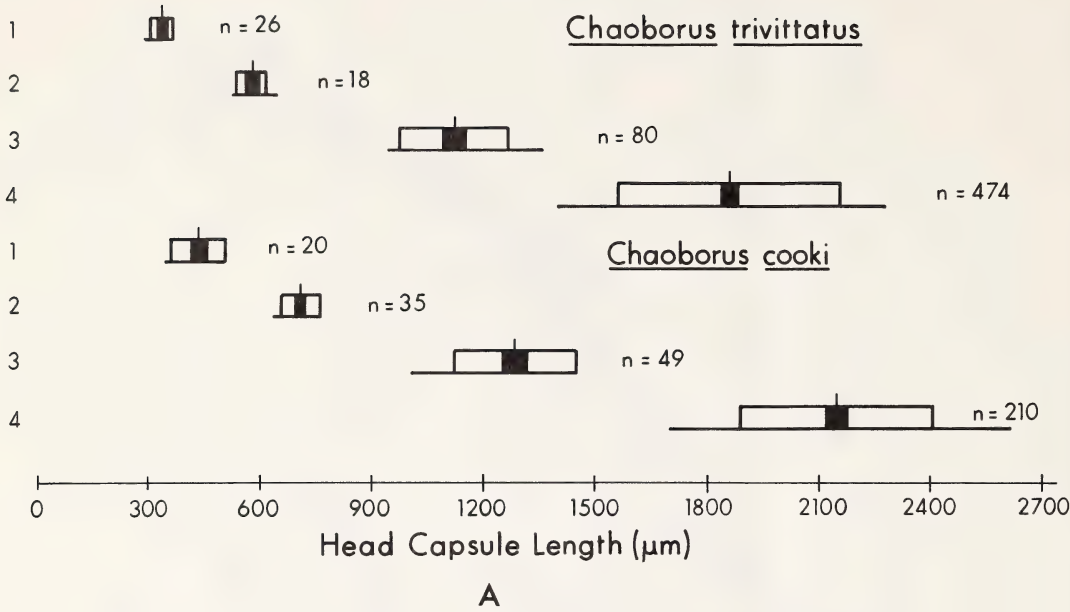
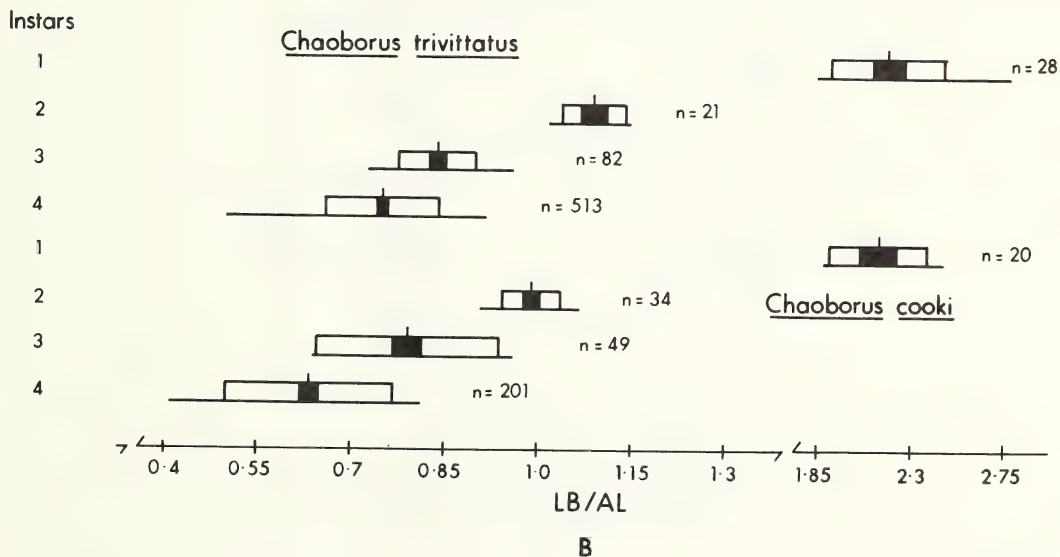
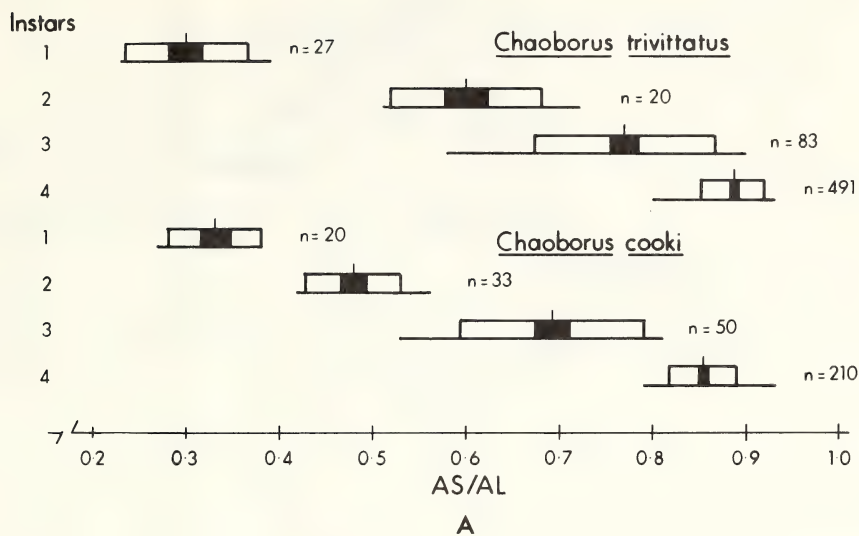


Figure 21. Variation of characters of larval instars of *Chaoborus trivittatus* and *Chaoborus cooki*. A. Head capsule length. B. Antennal length.

Figure 22. Variation of characters of larval instars of *Chaoborus trivittatus* and *Chaoborus cooki*. A. AS/AL. B. LB/AL.

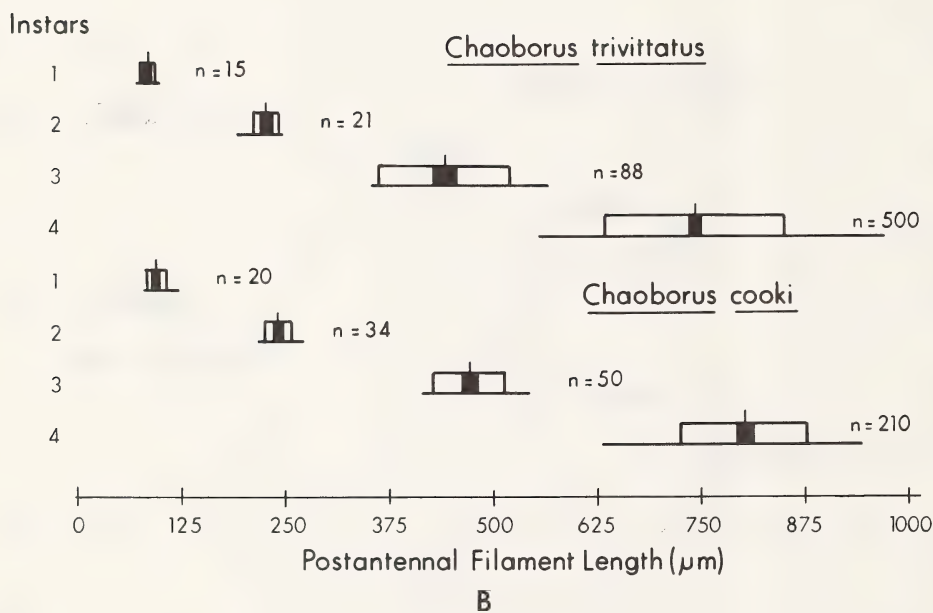
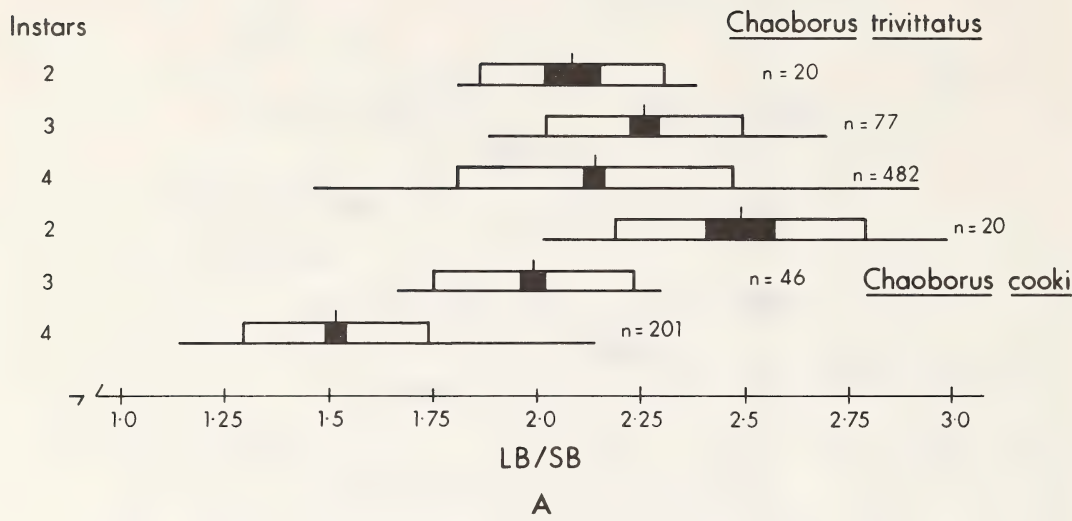


Figure 23. Variation of characters of larval instars of *Chaoborus trivittatus* and *Chaoborus cooki*. A. LB/SB. B. Postantennal filament length.

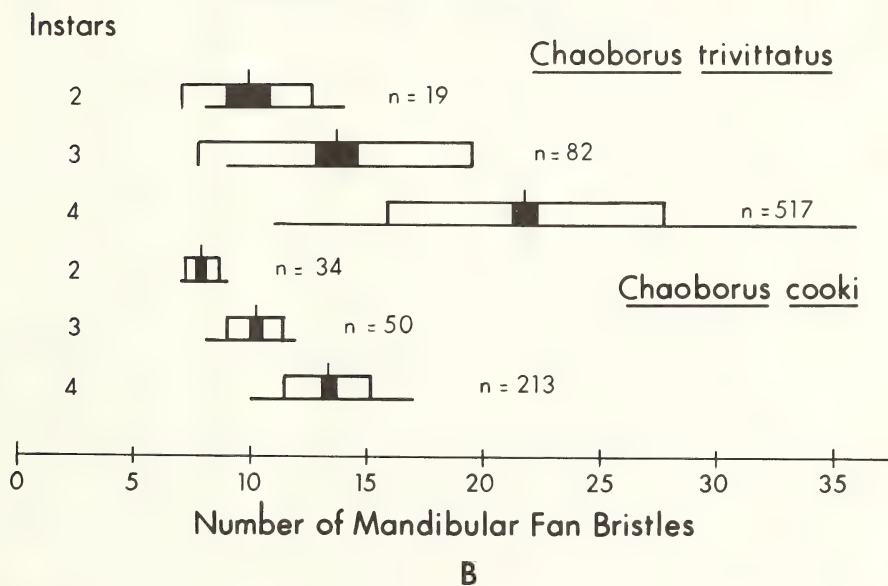
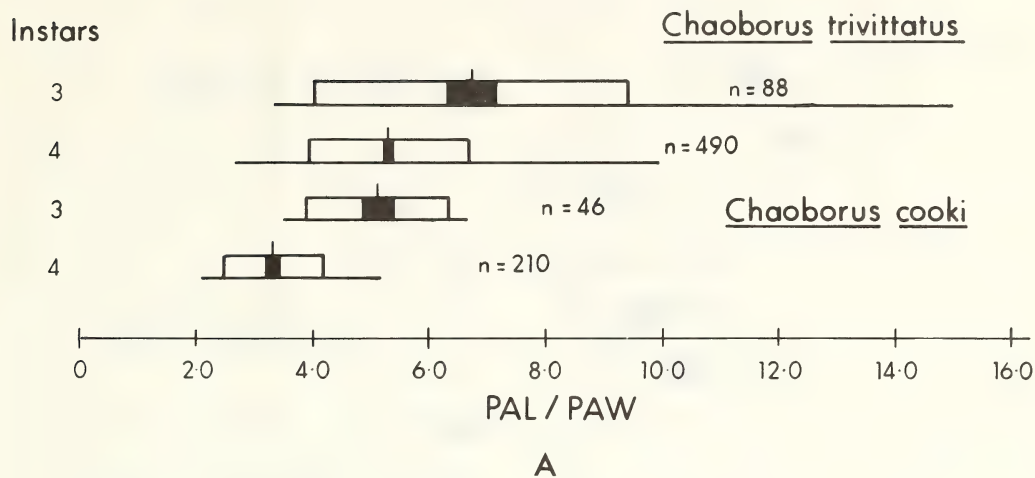
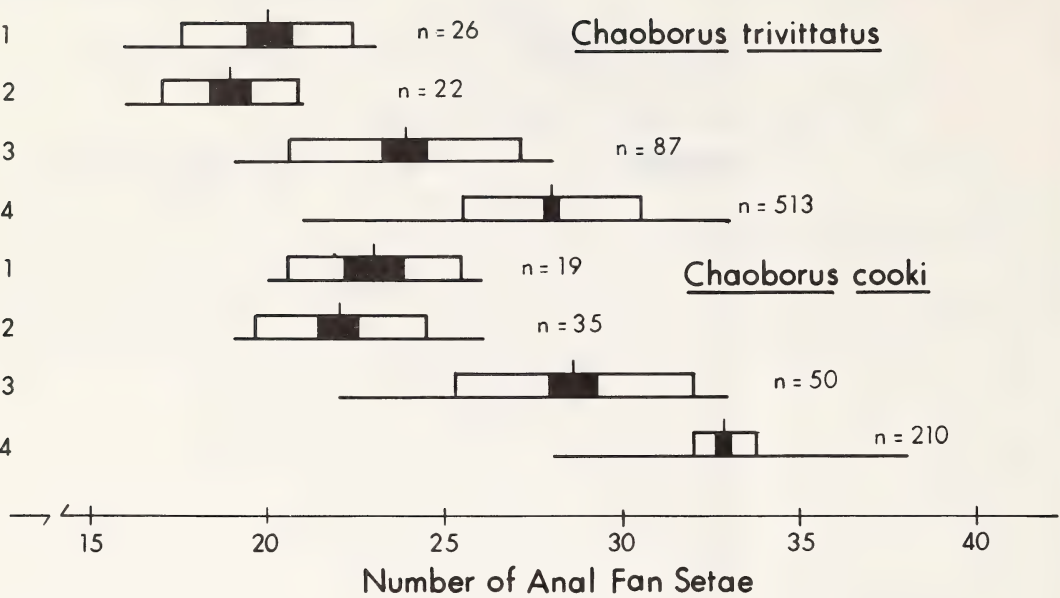
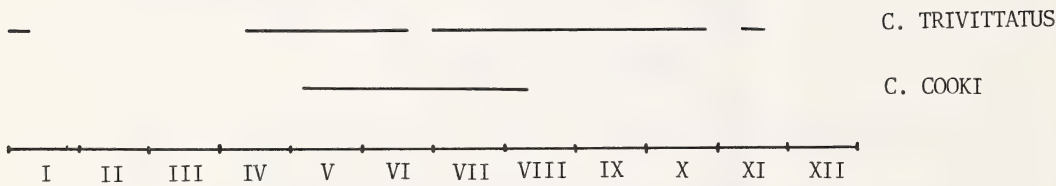


Figure 24. Variation of characters of larval instars of *Chaoborus trivittatus* and *Chaoborus cooki*. A. PAL/PAW. B. Number of mandibular fan bristles.

Instars

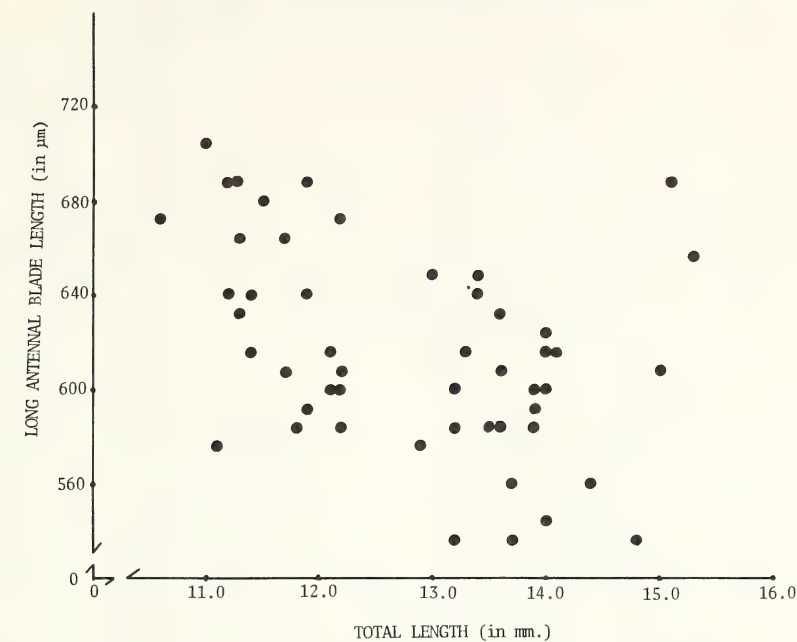


A

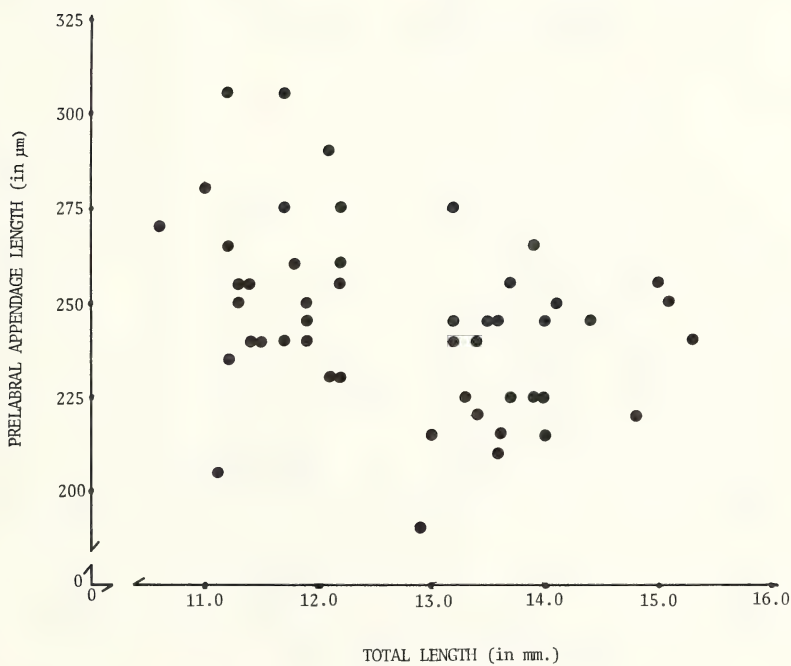


B

Figure 25. Variation of characters of larval instars of *Chaoborus trivittatus* and *Chaoborus cooki*. A. Number of anal fan setae. B. Temporal distribution of fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*.



A



B

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Figure 26. Age-related variation of male fourth instar larvae of *Chaoborus cooki*. A. Relationship between total length and long antennal blade length. B. Relationship between total length and prelabral appendage length.

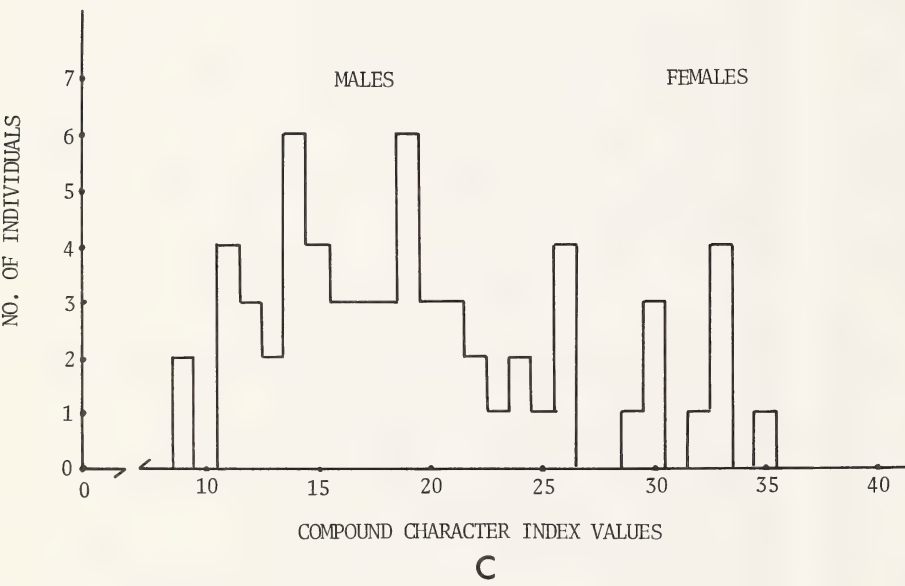
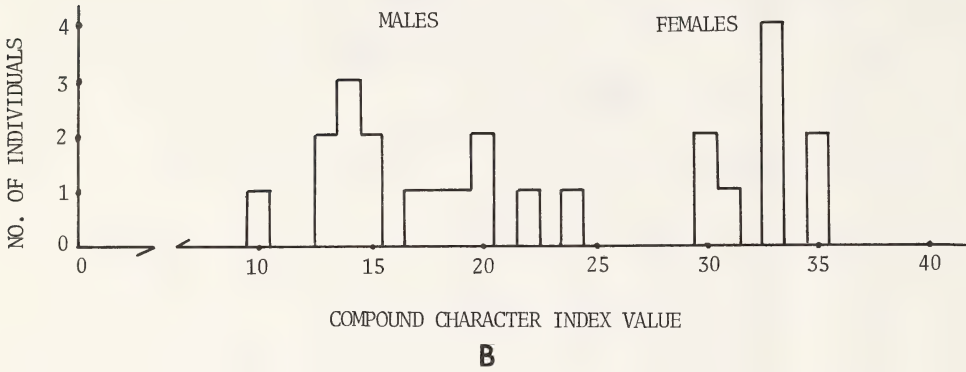
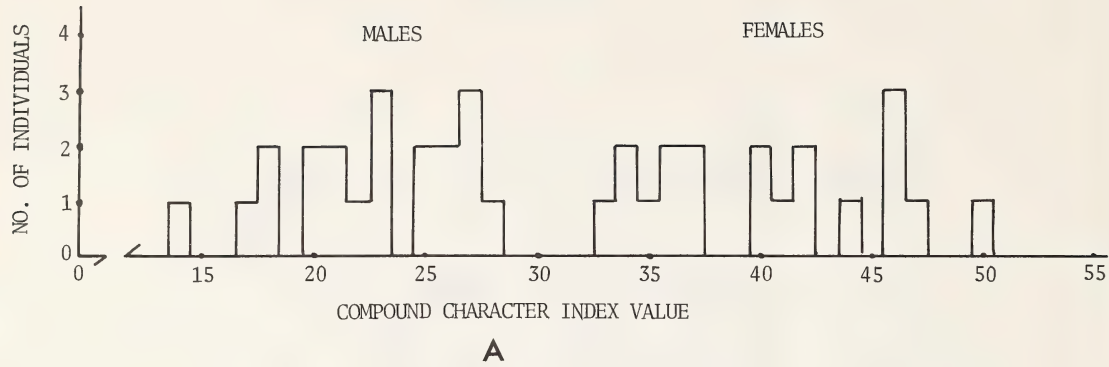
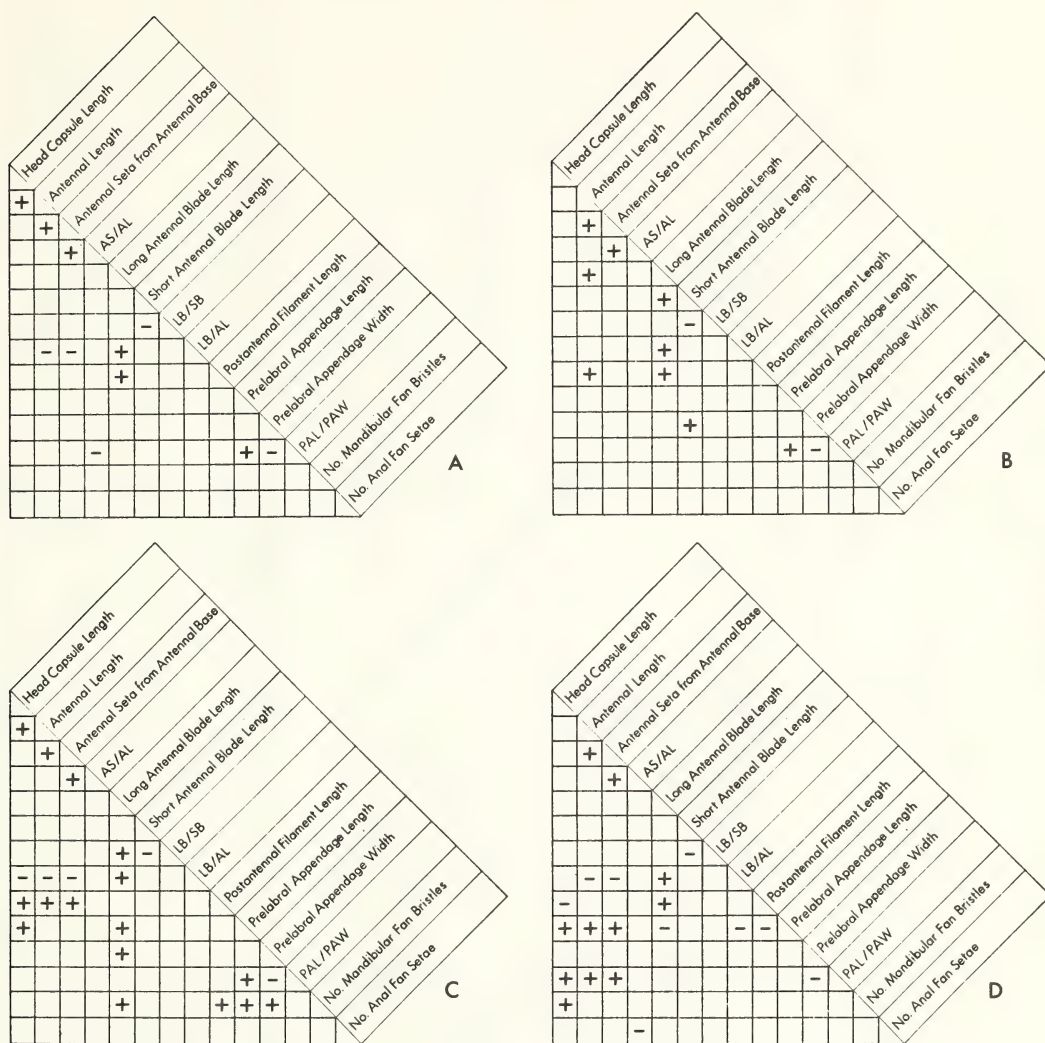


Figure 27. Results of compound character index used to sex fourth instar larvae. A. Of *Chaoborus trivittatus* from 2.4 km west of Edmonton, Alberta. B. Of *Chaoborus cooki* from 32 km west of Edson, Alberta. C. Of *Chaoborus cooki* from 1.6 km south of Jasper, Alberta.



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Figure 28. Correlation of characters of fourth instar larvae. A. Male *Chaoborus trivittatus* B. Female *Chaoborus trivittatus*. C. Male *Chaoborus cooki*. D. Female *Chaoborus cooki*. Open spaces represent lack of significant correlation; + and - signify positively and negatively significant correlations, respectively.

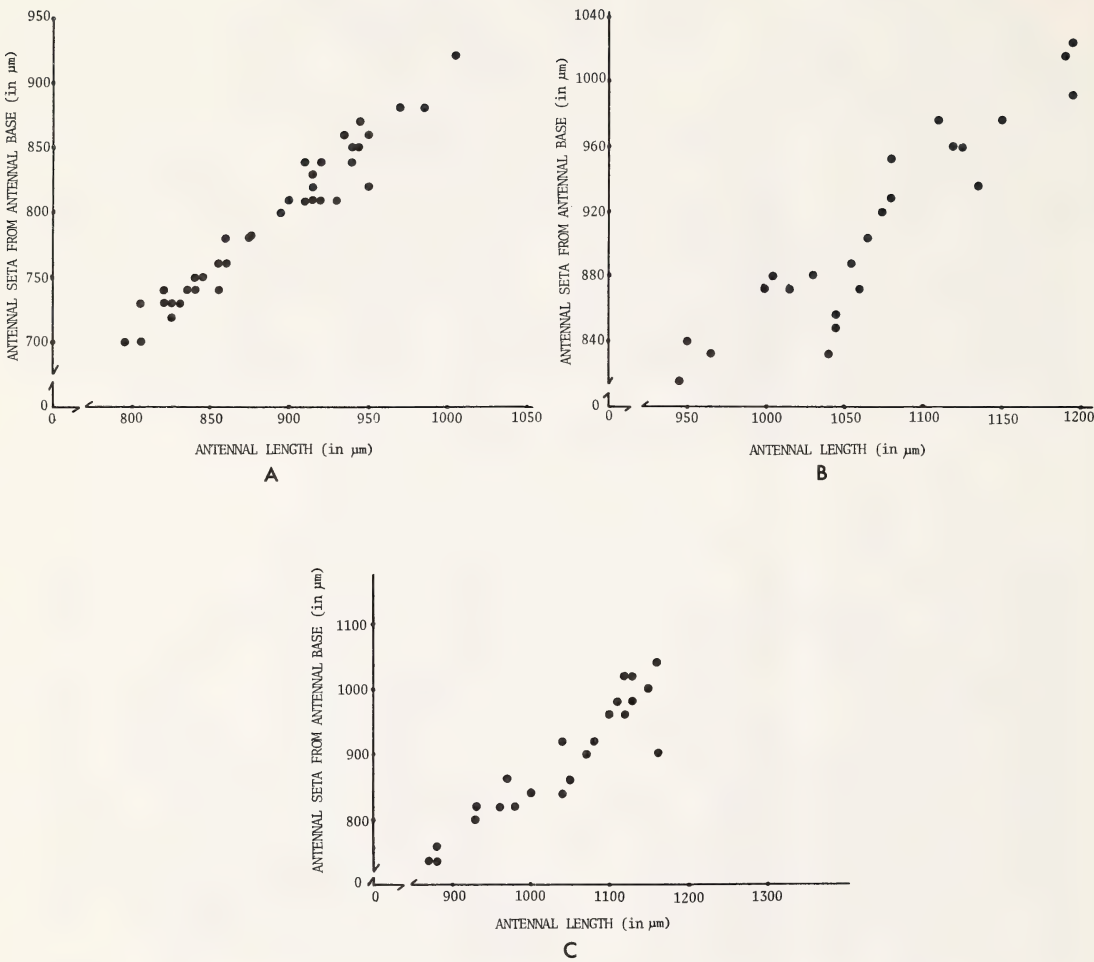


Figure 29. Relationship between antennal length and distance of antennal seta from base of antenna of fourth instar larvae. A. *Chaoborus trivittatus*. B. *Chaoborus cooki*. C. *Chaoborus nyblaei*.

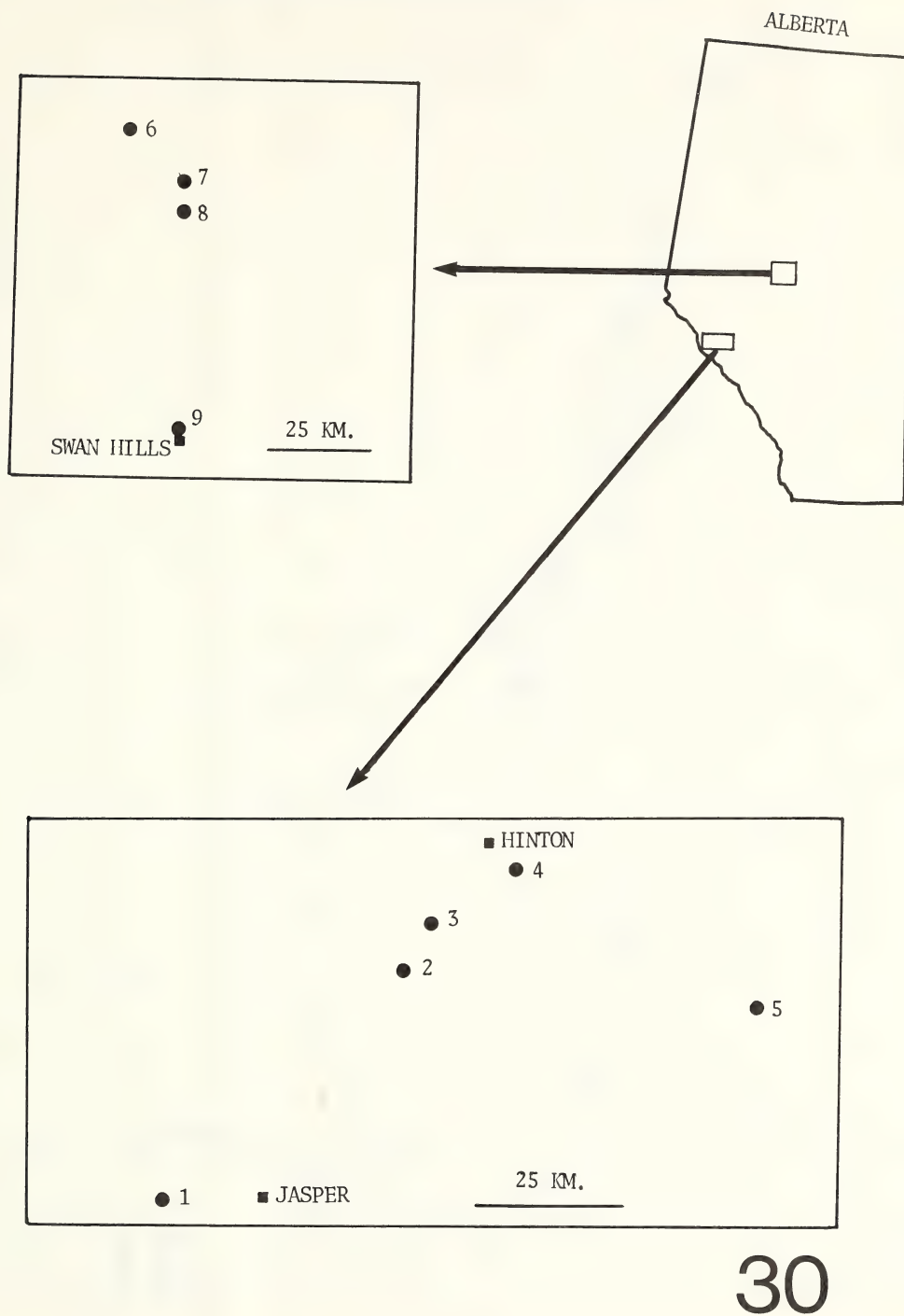


Figure 30. Localities of samples used to study geographical variation of characters of fourth instar larvae of *Chaoborus trivittatus* in Alberta. Samples from: 1. 16 km west of Jasper; 2. 45 km east of Jasper; 3. Pond nr. Kinky Lake; 4. 4.8 km south of Hinton; 5. 2.4 km south of Robb; 6. 69 km east of High Prairie; 7. 61 km north of Swan Hills; 8. 53 km north of Swan Hills; 9. 1.6 km north of Swan Hills.

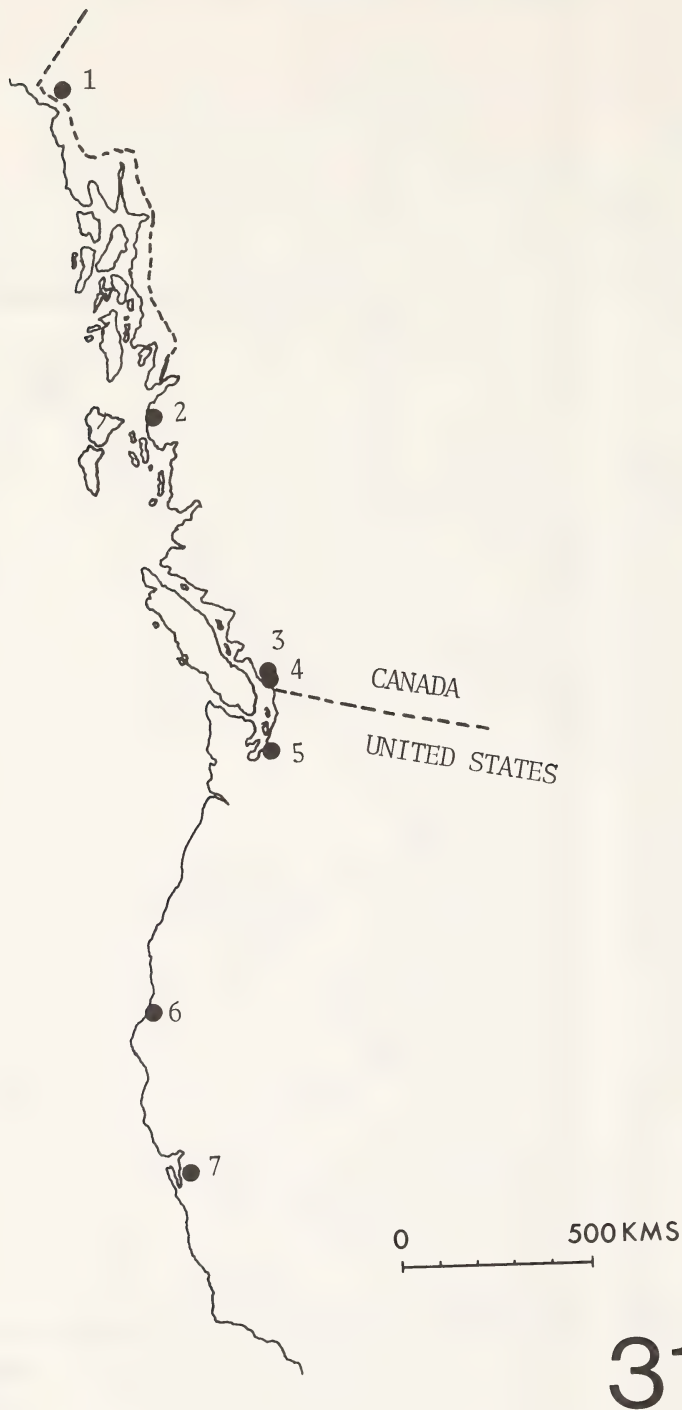
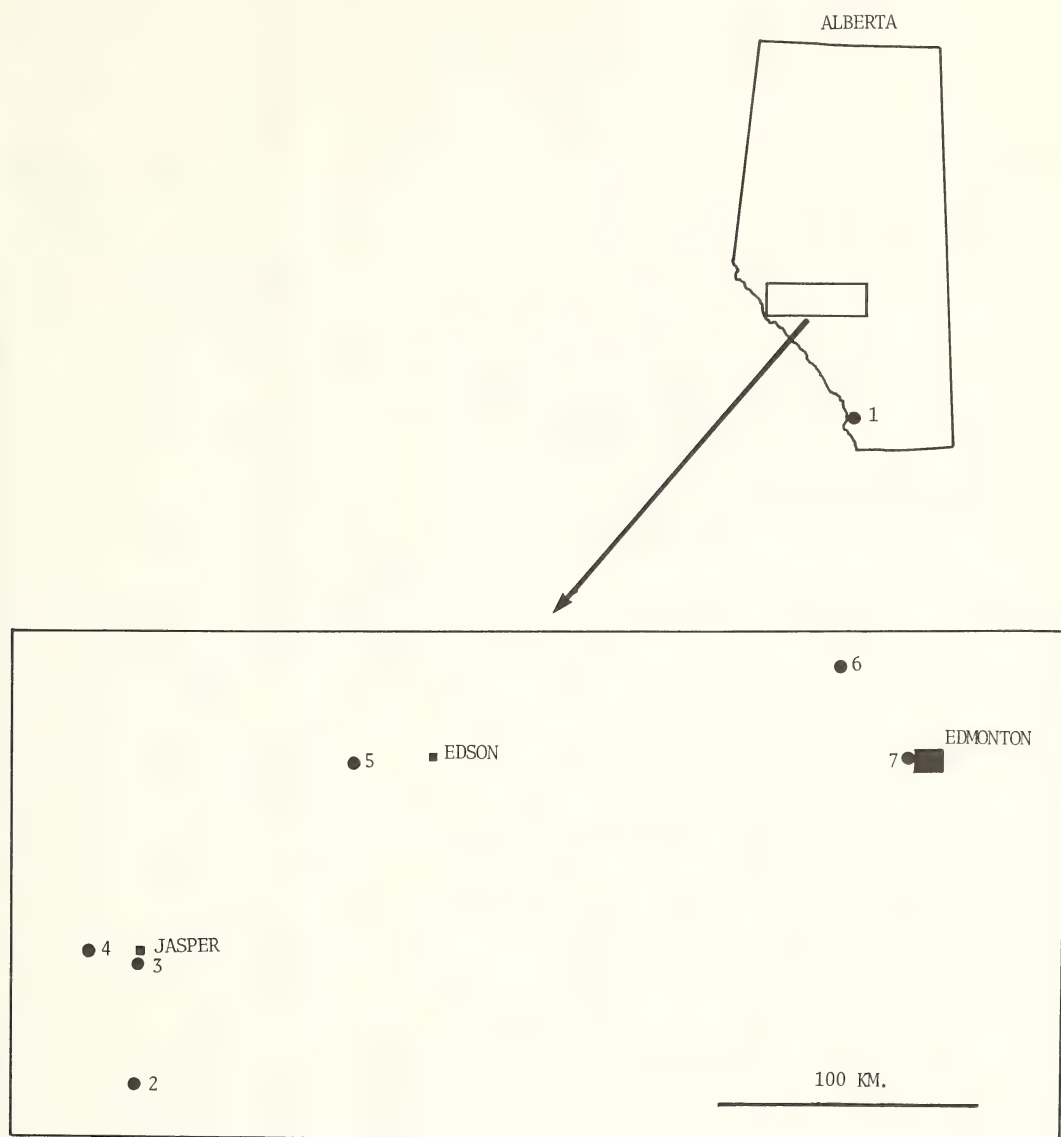


Figure 31. Localities of samples used to study geographical variation of characters of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. Samples from: 1. Klutlan Glacier moraine, Yukon Territory; 2. Prince Rupert, British Columbia; 3. Gwendoline Lake, British Columbia; 4. Eunice Lake, British Columbia; 5. Hall Lake, Washington; 6. Mad River, California; 7. Stanford and Jewel Lake, California.



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Figure 32. Localities of samples used to study geographical variation of characters of fourth instar larvae of *Chaoborus cooki* in Alberta. Samples from: 1. 69 km north of Coleman; 2. 53 km south of Jasper; 3. 1.6 km south of Jasper; 4. 6.4 and 23.3 km west of Jasper; 5. 32 km west of Edson; 6. 1.4 km west of George Lake; 7. 2.4 km west of Edmonton.

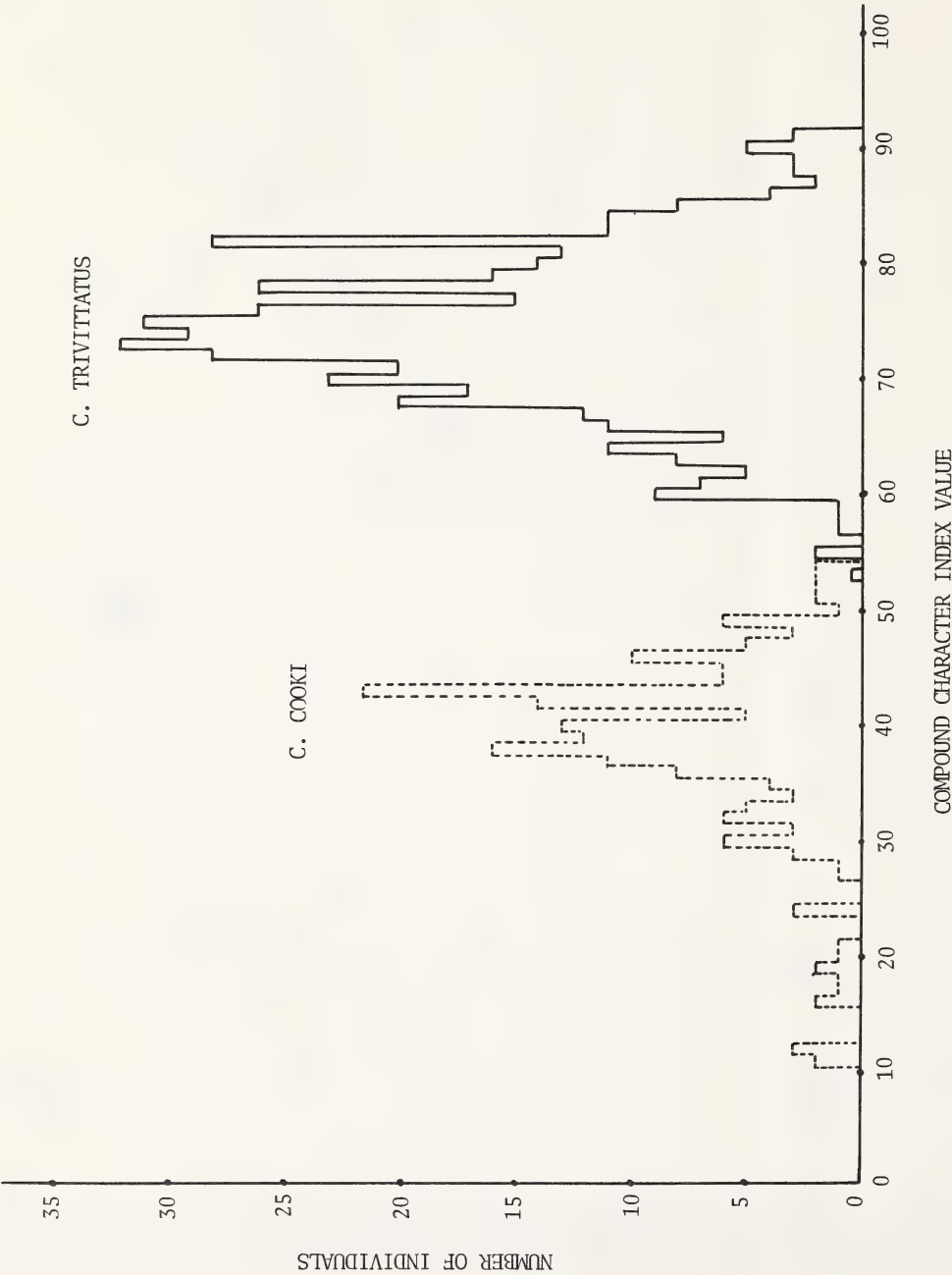
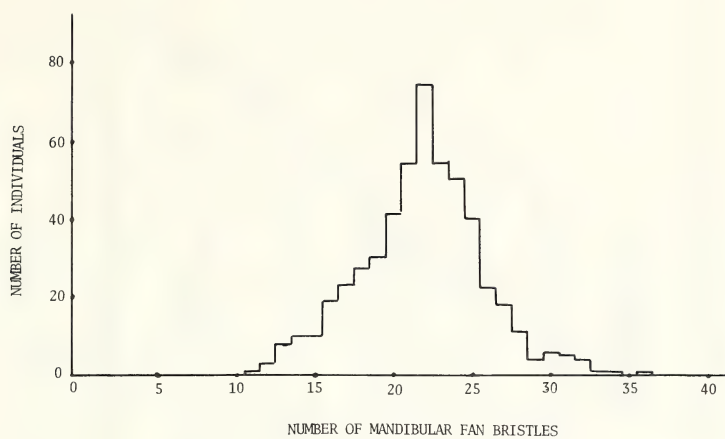
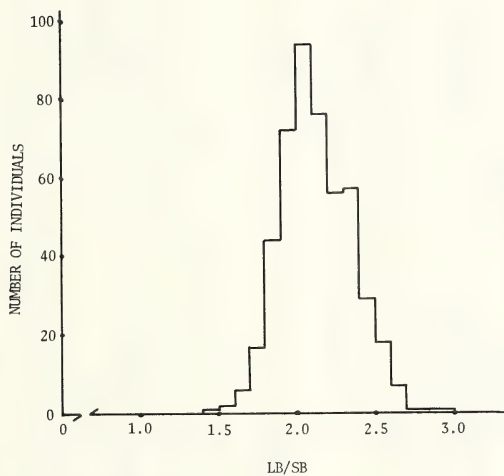


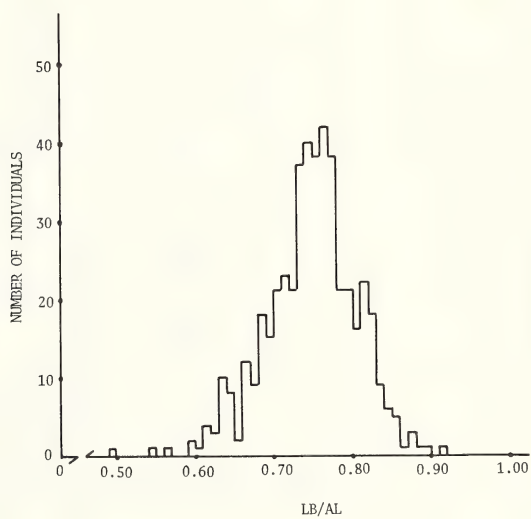
Figure 33. Results of compound character index used to recognize fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*.



A



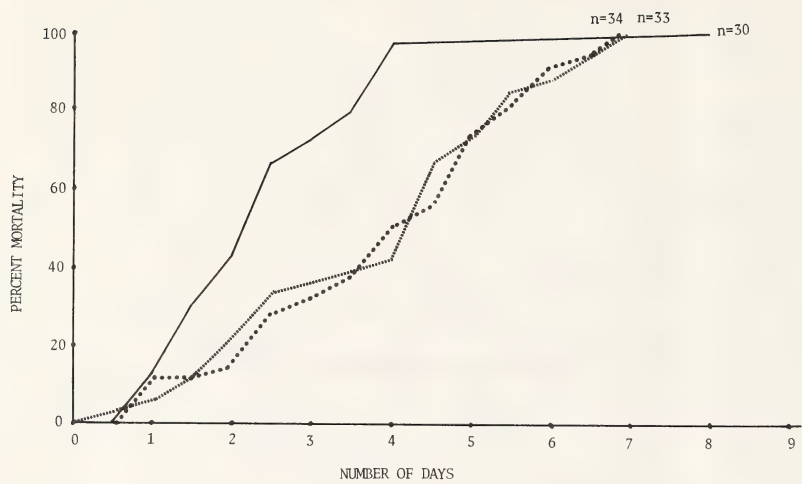
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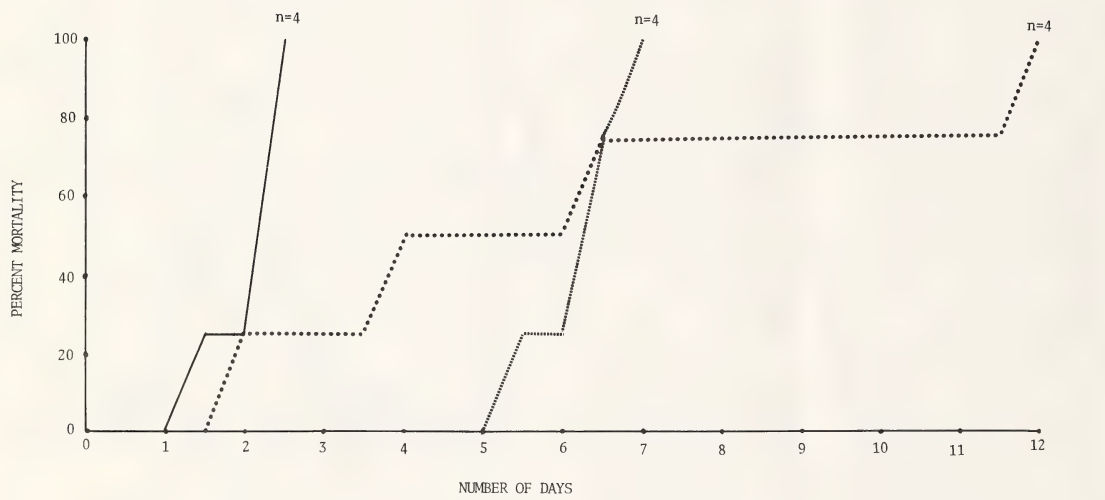
C

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Figure 34. Variation of characters of fourth instar larvae of *Chaoborus trivittatus*. A. Number of mandibular fan bristles. B. LB/SB. C. LB/AL.



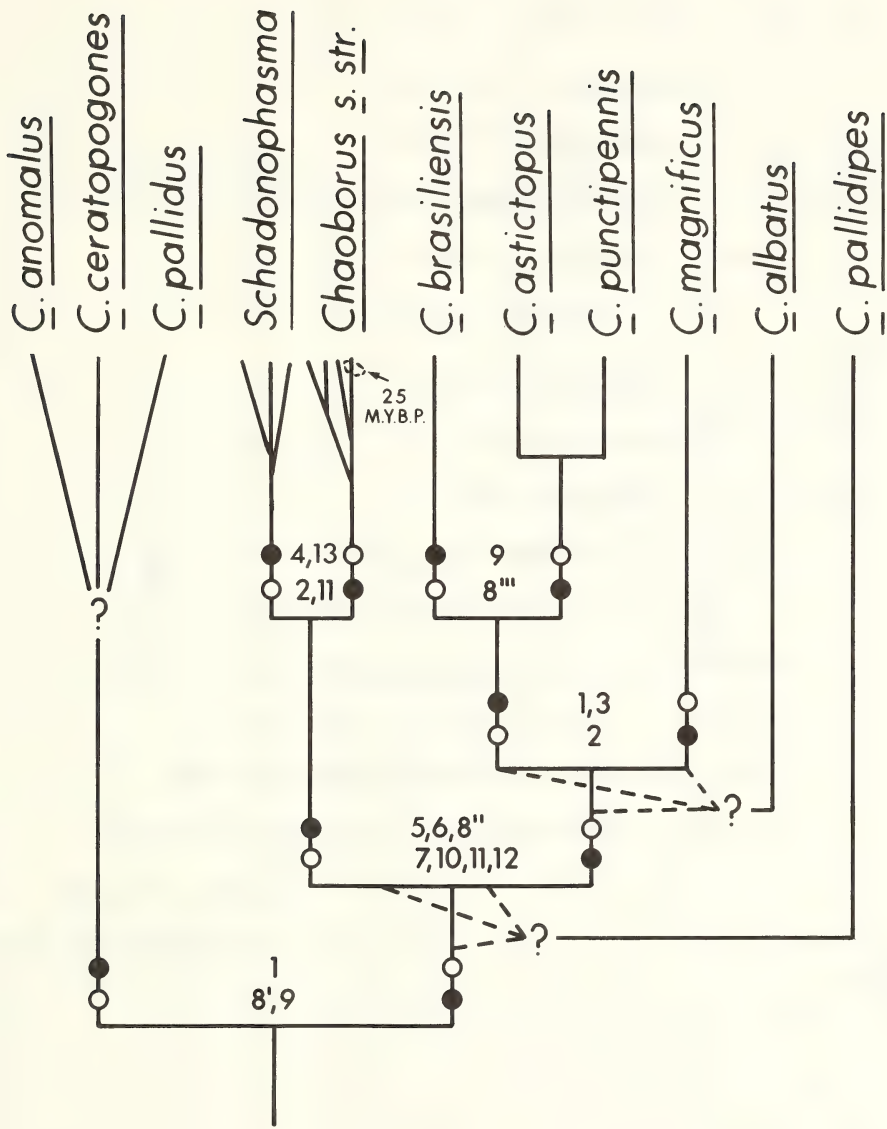
A



B

..... WITH WATER
- - - - - WITH DYED WATER
———— WITH INACCESSIBLE WATER

Figure 35. Mortality of adult *Chaoborus trivittatus*. A. Males. B. Females.



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Figure 36. Phylogeny of species of *Chaoborus*. Black circles signify apomorphie states, open circles plesiomorphie states. M.Y.B.P. indicates million years before present.

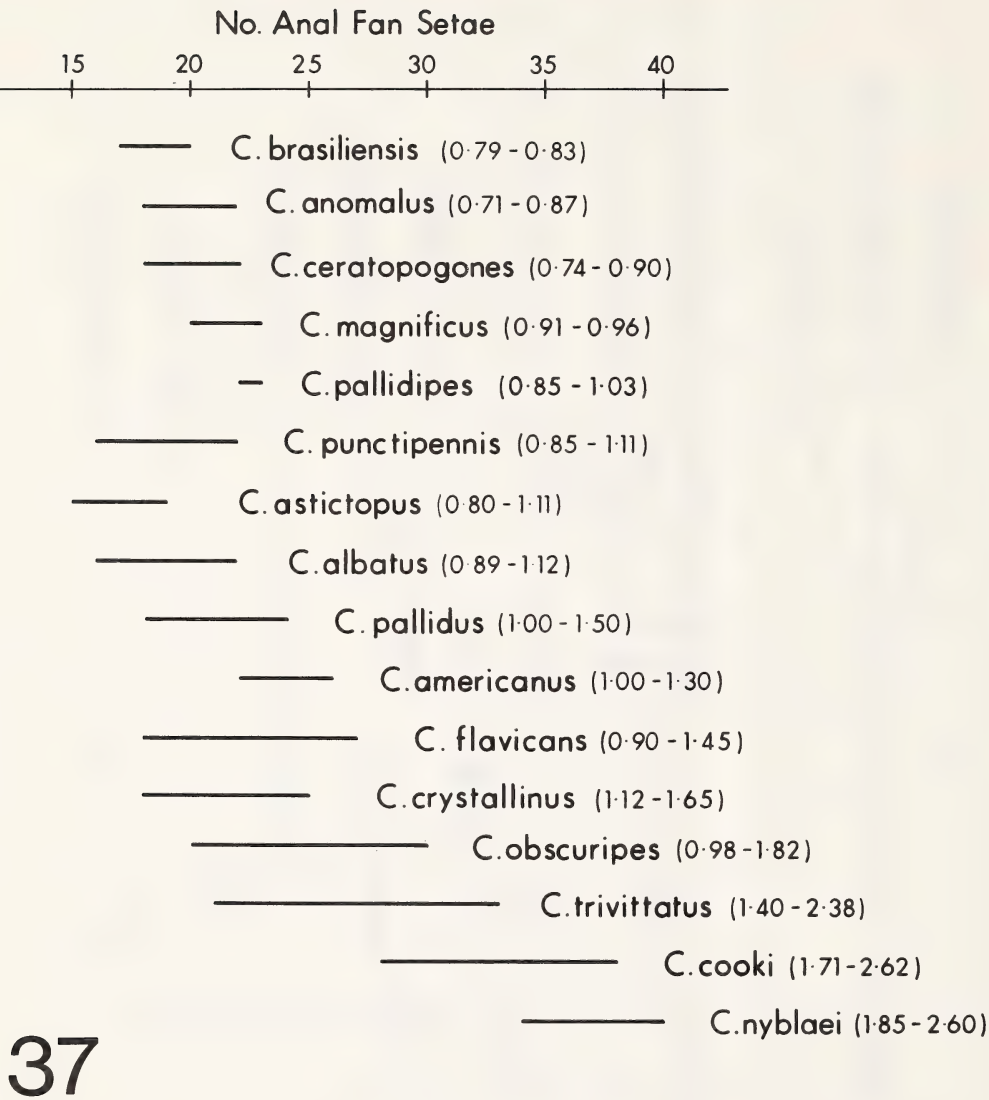
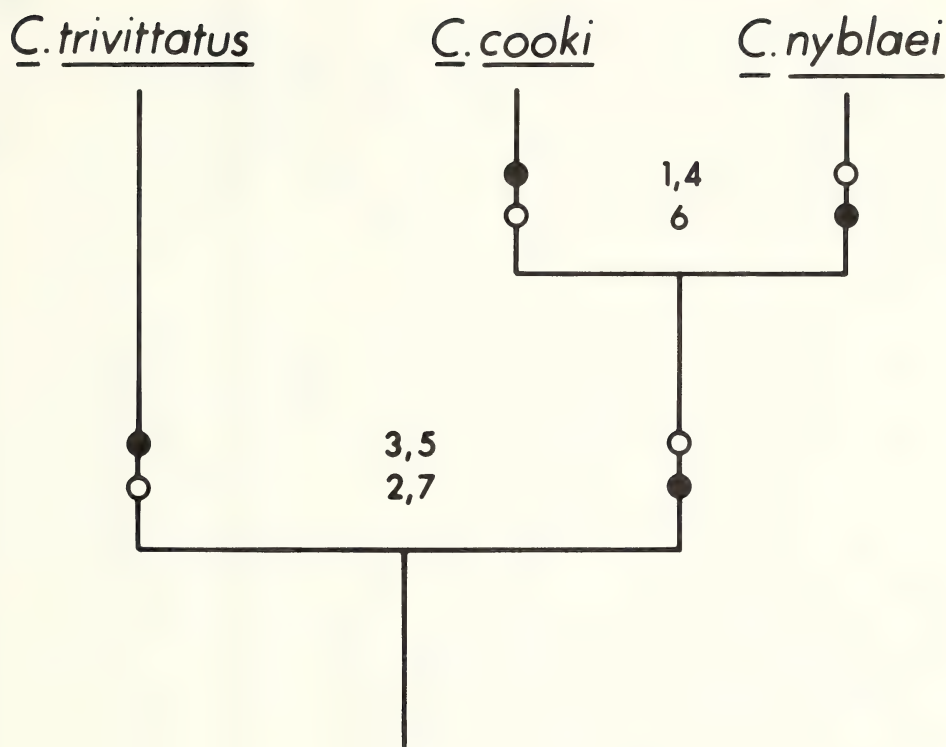


Figure 37. Relationship between number of anal fan setae and head capsule length (given in parentheses as mm) of fourth instar larvae of *Chaoborus* species.



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Figure 38. Phylogeny of species of *Schadonophasma*. Black circles signify apomorphic states, open circles plesiomorphic states.

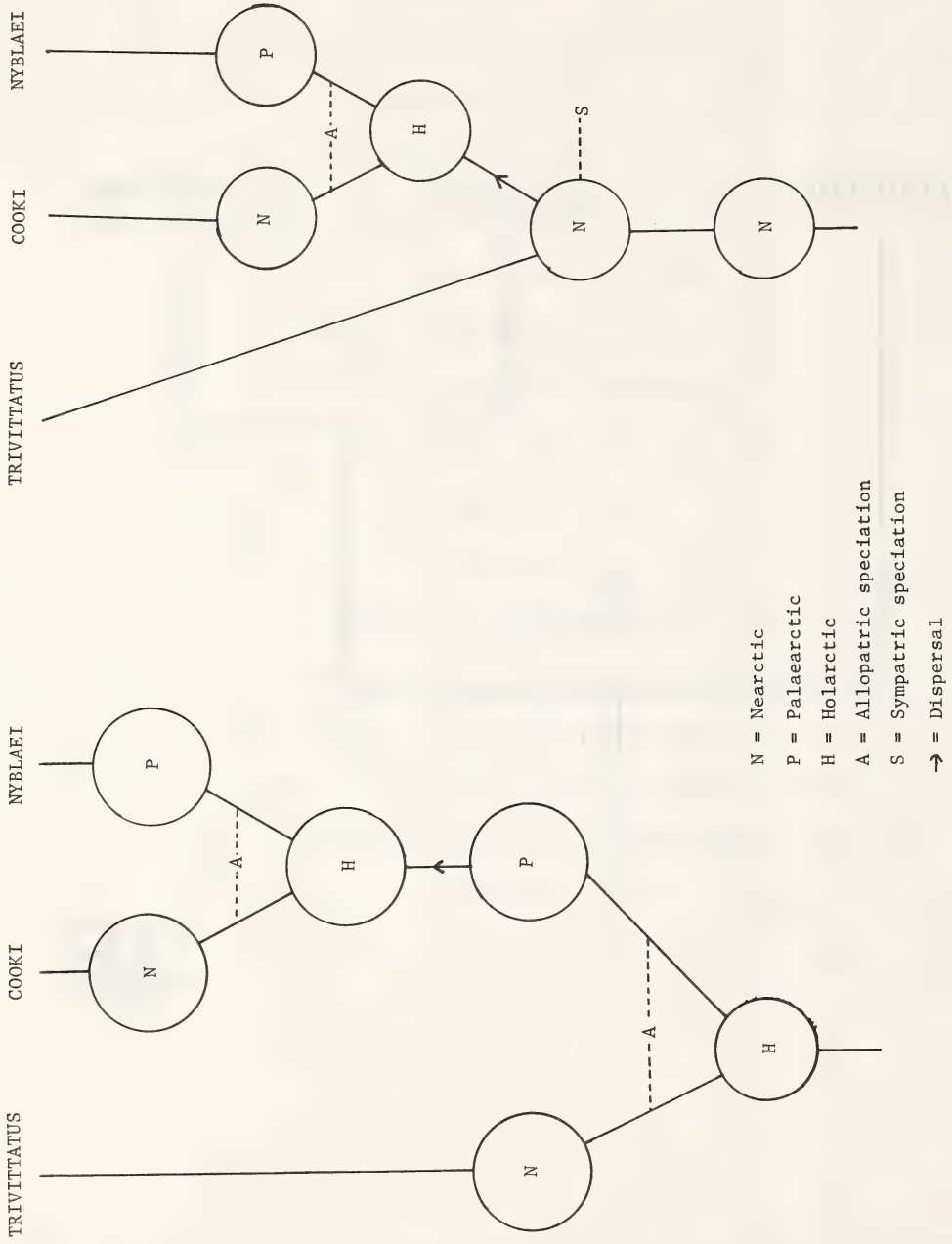
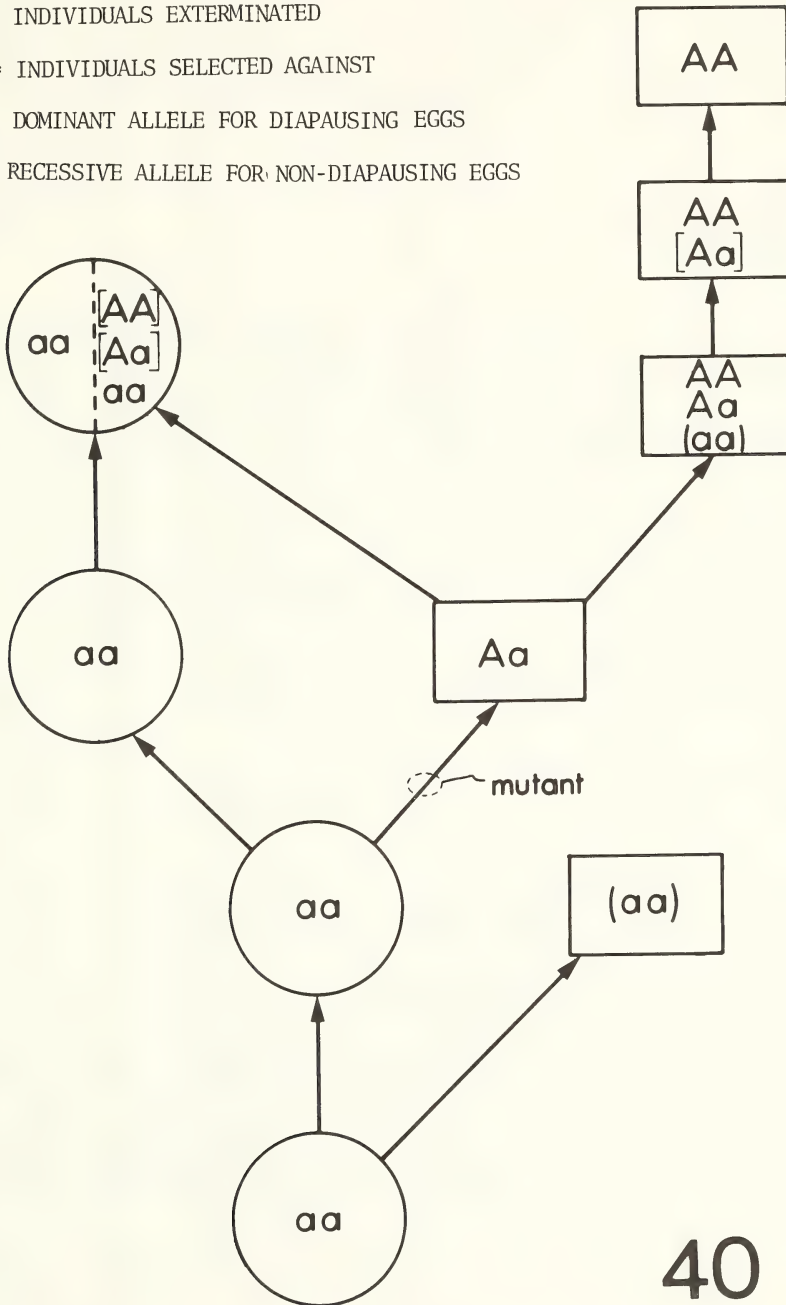


Figure 39. Schematic representation of alternative zoogeographic hypotheses for *Schodonophasma* species.

- = PERMANENT POND
 □ = TEMPORARY POND
 () = INDIVIDUALS EXTERMINATED
 [] = INDIVIDUALS SELECTED AGAINST
 A = DOMINANT ALLELE FOR DIAPAUSING EGGS
 a = RECESSIVE ALLELE FOR NON-DIAPAUSING EGGS



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Figure 40. Schematic representation of events of sympatric speciation of lineages giving rise to *Chaoborus trivittatus* and *Chaoborus cooki-nyblaei*.

EFFECTS OF TEMPERATURE AND RELATIVE HUMIDITY ON EMBRYOGENESIS IN EGGS OF *MAMESTRA CONFIGURATA* (WALKER) (LEPIDOPTERA: NOCTUIDAE)

M.P. JONES¹

Department of Entomology
University of Alberta
Edmonton, Alberta
T6G 2E3

B.S. HEMING

Department of Entomology
University of Alberta
Edmonton, Alberta
T6G 2E3

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15: 257-294 1979

Effects of various combinations of temperature and relative humidity on embryogenesis in eggs of Mamestra configurata (Walker) were investigated. The following temperature thresholds were determined for some stages of embryogenesis: developmental-hatching, (8.5 C), hatching, (5.0 C), developmental (between 0.0 and 2.0 C) and high temperature developmental-hatching threshold, (30.0 C). Temperature and rate of development curves were derived using three different relative humidities (0, 60 and 98%) and a range of temperatures (8.5–30.0 C). Length of exposure to 35.0 and 5.0 C required to produce mortality of 50% and 95%, was determined for eggs of various ages. The age of eggs exposed to 35.0 C did not appear to influence mortality, but was very important in eggs exposed to 5.0 C. The older the eggs, the longer the exposure required to produce 50% and 95% mortality. The effects of daily exposure to 35.0 C and 5.0 C were studied for eggs of various ages. Older eggs could tolerate longer daily exposure to 35.0 C without high mortality than could younger eggs but, when total length of exposure was determined, there was no significant difference in tolerance between older and younger eggs. Daily exposure to 5.0 C had little effect on mortality but lengthened development.

The developmental rate and temperature curve for eggs of Mamestra configurata is J-shaped. Practical application of this curve to field populations will increase the accuracy of larval surveys.

Nous avons étudié les effets de diverses combinaisons de température et d'humidité relative sur l'embryogénèse des oeufs de Mamestra configurata Walker. Nous avons déterminé les seuils de température pour quelques stades de l'embryogénèse: la température minimale permettant le développement complet de l'oeuf et son éclosion est 8.5 C, et la température maximale est 30.0 C; la température minimale pour l'éclosion seulement est 5.0 C, la température minimale à laquelle l'embryon se développe (sans éclore) se situe entre 0.0 et 2.0 C. Nous avons étudié le taux de développement en fonction de la température (entre 8.5 et 30.0 C) sous trois conditions d'humidité relative (0, 60 et 98%). Nous avons déterminé, pour des oeufs d'âges divers, les durées d'exposition à 35.0 C et 5.0 C causant 50% et 95% de mortalité. A 35.0 C, l'âge des oeufs ne paraît pas affecter la mortalité, mais à 5.0 C, son effet est important: plus les oeufs sont âgés, plus longue est la période d'exposition requise pour obtenir 50% et 95% de mortalité. Nous avons étudié les effets d'expositions journalières à 35.0 C et à 5.0 C sur des oeufs d'âges divers. Les oeufs plus âgés peuvent tolérer une plus longue exposition journalière à 35.0 C que les jeunes oeufs, sans qu'en résulte une mortalité élevée; mais lorsqu'on considère la durée totale d'exposition, on n'observe aucune différence significative entre la tolérance des oeufs âgés et celle des jeunes oeufs. L'exposition journalière à 5.0 C affecte peu la mortalité, mais prolonge le développement embryonnaire.

Le taux de développement des oeufs de M. configurata en fonction de la température suit une courbe en forme de "J". L'application d'une telle courbe aux populations naturelles permettra d'obtenir des estimés plus précis de l'état des populations larvaires.

¹Present address: South Peace Senior Secondary School, Dawson Creek, British Columbia.

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INTRODUCTION

Moths of the species *Mamestra configurata* (Walker) (Lepidoptera: Noctuidae), the Bertha armyworm, occur from Mexico City, Mexico in the south (King, 1928) to Keg River, Alberta in the north (Philip, pers. comm). Within this range, the species is of economic importance only in Western Canada and in the State of Washington.

The species was first cited in the economic entomological literature in 1928 in a paper by King (1928). That paper dealt with external structure of the various lifestages, with some aspects of its life history including geographic range and host plants, (rape was not included), and included descriptions of larval damage on various crop plants. His larval and pupal descriptions are still helpful in separating specimens of *Mamestra configurata* from those of other noctuids causing damage to rape.

In Alberta, the species has one generation per year (Beirne, 1971). Eggs are deposited by the females on leaves of host plants early in July. Larvae feed on these until about three-quarters grown and then chew into the flowers, seed pods, bolls or fruit in August and early September. Larvae pupate in the soil and overwinter, emerging as adults the following June and July.

Embryogenesis in eggs of *Mamestra configurata*, from pre-fertilization to eclosion, has been described by Rempel (1951) who mentioned ovipositional habits of this moth and enlarged upon King's (1928) observations of its eggs. One of the more important observations Rempel made, which had important implications for our research was that fertilization at room temperature (20.0 C – 21.0 C) occurred in the second half hour after oviposition.

The serious outbreaks in 1971 and 1972 of larvae of this species on rape (*Brassica campestris* L. and *Brassica napus* L.) stimulated numerous studies, the results of which are now being published.

The male pheromones of *Mamestra configurata* have been studied by Clearwater (1975a,b) and those of females by Struble *et al.*, (1975). Clearwater (1975c) also described the structure and postembryogenesis of the male pheromone system. Bodnaryk (1978) investigated factors affecting diapause development and survival of pupae and Bailey (1976), the effects of temperature on non-diapause development.

In Western Canada, the importance of *Mamestra configurata* increased in 1971 and 1972, partly because of a large increase in rape acreage. After the first serious outbreak of this insect in 1971, the Alberta Department of Agriculture instituted a series of four annual surveys to determine, first, the areas where densities of *Mamestra configurata* were high and where the potential for economic damage great, and second, to follow the changing distribution of these populations in Alberta each year.

A fall pupal survey was conducted in areas where outbreaks occurred that year, and its results enabled estimates to be made about the initial size of overwintering populations. A second pupal survey was conducted in the spring to ascertain winter mortality of overwintering populations. A third survey,

conducted from mid-May until the end of September, involved the use of black light traps to monitor adult emergence and abundance. Larval surveys were conducted in July in areas where light trap captures were considered high, and first and second instar larval populations were monitored 14–21 days after peak adult activity. Based on results of these surveys, a series of maps were prepared which indicated areas of potential economic damage for that crop year. The most important survey was the final one because this confirmed the presence of the damaging larval stage in the field.

The principal weakness of the final survey is its timing. For it to be effective, it should be conducted at a time when the majority of eggs have hatched, but before the larvae have reached a size where they are causing economic damage. If the survey is conducted too early before most of the eggs have hatched, the population estimate resulting may be too low. If left until too late, it may be impossible to devise and implement control measures before considerable damage has occurred.

There were three principal objectives in undertaking this study: (1) to remove some of the guess-work involved in timing the egg and larval survey by developing temperature curves for embryogenesis which could aid in predicting probable hatching time of eggs in the field, (2) to determine the effects on development and viability of eggs exposed to various periods of unfavourable temperature, and (3) to determine the effect of relative humidity on embryonic development in this insect.

GENERAL METHODS

Handling and collecting eggs

Collecting large numbers of eggs of known age was essential for much of the experimental work. The following procedures were used to facilitate collection and aging of these eggs. All eggs used in the following experiment were obtained from moths reared from field-collected pupae.

Eggs for stock use. – Moths were placed in cages containing four rape plants and subjected to a photoperiod of 16L:8D. Eggs were collected once a day at the end of the dark period by removing leaves containing egg clusters. Often it proved necessary to break the clusters into smaller units. The adhesive which binds the eggs to the leaves was softened with distilled water and individual eggs were removed by gently pushing them with a camel hair brush.

Collecting accurately-timed eggs. – A stock culture of male and female moths was caged in a growth chamber at 20.0 C and approximately 60% RH (for some experiments a culture was maintained at 15.0 C). The moths were fed a 10% honey and water solution from wicked containers, the solution being changed twice a week. Since adults of *Mamestra configurata* generally oviposit at night, we reversed the normal photoperiod so that darkness occurred between 0800 and 1600 hours.

Females prefer a rough substrate for oviposition, but, given no choice, will oviposit on almost any surface. Plastic sandwich wrap was avoided by females, probably because they were unable to find a purchase on it. If the cage is lined with this material, the moths show strong ovipositional preference for paper towelling or other rough textured materials. Paper toweling was chosen as the ovipositional substrate because of its availability and ease of handling. The towelling was folded in such a manner that it was able to stand on its own. It was introduced into the cage approximately one hour after dark and replaced 1 3/4 hours later.

Once the paper towelling was removed, egg clusters were examined at X12 magnification under a binocular microscope and were separated into groups of the desired number of eggs with a razor blade. The strips containing eggs were quickly examined and any damaged eggs were discarded. Each strip was then placed in a clean, 1 mm cap vial, ready to be used in the experiment. The top of each vial was covered with plastic screening, held secure by a rubber band. Any eggs remaining from an egg cluster were placed in a vial marked to indicate their origin and were used to check fertility for that group.

EXPERIMENTS AND RESULTS

Development of eggs

Eggs of *Mamestra configurata* are generally deposited on the underside of leaves of the host plant in a tight, single-layered cluster and are oriented with their anterior, micropylar ends pointed away from the substrate (Rempel, 1951). They are yellowish white when first deposited, but become off-white several hours later. Approximately 24 hours later (at 20.0 C), a band of brown pigment appears around the equator of fertile eggs with additional small patches developing in the micropylar area (Rempel, 1951). Approximately eight hours prior to hatching, the egg turns jet black as the larval head capsule becomes visible through the transparent chorion — a stage referred to as the “black spot stage” by Peterson (1964). A more detailed description of the egg was given by Jones (1977).

Viability and size of field-collected versus laboratory deposited eggs

The main purpose of this experiment was to determine if laboratory rearing and handling techniques influenced egg viability or numbers laid when compared to eggs deposited under field conditions.

Methods. — A laboratory culture of adult moths was maintained in a growth chamber at 20.0 C \pm 0.5 C and approximately 60% RH. The photoperiod maintained was 16L:8D, a close approximation of field conditions at the time of the experiment. The moths were provided with potted rape plants for oviposition, these being at approximately the same stage of development as were field sown plants. Ten egg clusters of unknown age were removed at random from the caged culture by removing the leaf with the cluster. Each cluster was then divided carefully into groups of 15 eggs as previously mentioned and these placed in 1 mm cap vials. When less than 15 eggs remained, the remaining group was also placed in a 1 mm cap vial. Eggs from each cluster were kept separate so that mortality and number of eggs could be recorded for each cluster.

Field samples of eggs were studied in a field of rape near Lacombe, Alberta. Ten egg clusters, of unknown age, were located and counted and the leaf with each was encased in a fibre-glass screen having a mesh size of 16 threads per cm to prevent access of predators, parasites and larval escape. These cages were inspected twice daily and the number of hatched larvae recorded for each cage.

Results. — The results of this experiment are recorded in Table 1. Although egg viability (97%) did not differ significantly between the two groups, the average size of the laboratory clusters (146.5) was significantly larger than that of field clusters (80.8). Bailey (1976) reported that females of *Mamestra configurata* reared for ten generations on an artificial diet deposited 40–60 eggs per cluster with viability of eggs ranging from 90–97% at temperatures from 8.0–28.0 C.

Temperature thresholds for embryogenesis

Insect embryogenesis is influenced by many external factors which, acting separately or together, restrict developmental potential. Within the range of each of these factors are points designated as thresholds. Continual exposure of an embryo to the factors beyond these points eventually results in death.

One of the most important and easily studied factors influencing embryogenesis is temperature. Insects, being poikilothermic, are greatly affected by ambient temperature. However, only the egg and the quiescent pupal stage are unable to move to a different microclimate to avoid temperature extremes. For this reason, eggs and non-mobile pupae are superior to other stages for study of temperature thresholds.

Table 1. Comparison of size of egg clusters and viability between laboratory and field collected eggs of *Mamestra configurata*.

Field Collected			Laboratory Collected		
No. of eggs	No. hatched	% hatch	No. of eggs	No. hatched	% hatch
56	53	94.64	130	128	98.46
78	75	96.15	189	186	98.41
86	85	98.84	254	247	97.24
42	38	90.48	127	123	96.85
28	28	100.00	95	94	98.95
187	186	99.46	102	99	97.06
119	118	99.16	79	73	92.96
97	95	97.94	163	159	97.55
63	61	96.82	129	129	100.00
52	50	94.34	197	190	96.45
80.8*	78.9	96.82	146.5*	142.8	97.03

*means significantly different based on T-tests ($P < 0.01$).

The developmental threshold. – The developmental threshold is the temperature at which, on the descending scale, development definitely ceases, and at which, on the ascending scale, development begins (Peairs, 1927). Knowledge of this threshold is vital if one is attempting to predict development on the basis of temperature. An experiment was conducted to determine this threshold for embryos of *Mamestra configurata*. Histological studies were made simultaneously.

Methods. Eggs used in this experiment were collected from clusters of over 100 deposited by females maintained at 15 ± 0.5 C. Eggs were placed at experimental temperatures of 0 ± 0.5 C, 2 ± 0.5 C and 4 ± 0.5 C when less than 30 minutes old, thus ensuring (based on Rempel's 1951 paper) that no prior development had occurred.

Two separate clusters of eggs were placed at each temperature. The eggs from each cluster were divided into 20 groups of five eggs each, each group of five being placed in a separate 1 mm cap vial (the eggs of the two clusters were kept separate). All but two vials were placed on a platform in a 160 mm desiccator containing a saturated salt (KNO_3) solution (Winston and Bates, 1960) to maintain the humidity at about 96%. Eggs in one of the remaining vials were fixed immediately in hot, alcoholic Bouins solution while the other vial was removed and placed at room temperature to determine if all its contained eggs were fertile.

Hot alcoholic Bouins was poured into one vial from each group daily for the first five days. After that time eggs were fixed at five day intervals. Standard histological techniques were used to prepare the eggs for staining with Delafield's Haematoxylin and Mallory's Triple Stain (Humason, 1972).

The experiment was concluded when histological signs of development were found in two or more eggs from both vials.

Results. The temperature developmental threshold for embryogenesis of *Mamestra configurata* is between 0.0 and 2.0 C.

Eggs at 4.0 C showed recognizable development after ten days and at 2.0 C after 15 days. No sign of development occurred at 0.0 C even after 40 days (data from eggs kept after end of experiment).

The hatching threshold. – The hatching threshold is the lowest temperature at which hatching of a fully developed larva can occur (Johnson, 1940).

The egg of *Mamestra configurata* is an excellent subject for this type of experiment because darkening of the head capsule always indicates that development is complete and that hatching is soon to follow.

Methods. Three egg clusters, less than one day old, and each containing in excess of 150 individuals, were collected over a period of two days from the stock culture. Each cluster was divided into groups of 50. Surplus eggs from each cluster were placed in 1 mm cap vials and labelled according to their cluster of origin. These eggs were used as spares to be substituted for any infertile eggs in the experimental group. Each of these nine groups of 50 eggs was placed in a 4 mm glass cap vial and labelled so that groups from individual clusters could be identified. All vials were then placed on a platform, at 20.0 C in a 160 mm desiccator which had been partially filled with distilled water to raise the humidity to greater than 90%.

The eggs were observed closely and were allowed to develop to the black head capsule stage. Then, to prevent larval escape, the tops of the vials were covered with a piece of plastic screening, secured by a rubber band. One vial from each egg cluster was then quickly transferred to identical, water-filled desiccators located in incubators set at temperatures of 7.5 ± 0.5 C, 5.0 ± 0.05 C and 2.5 ± 0.5 C. Eggs were observed twice daily and total number of hatched eggs recorded. The eggs were maintained at the experimental temperature for a maximum of 30 days after which they were returned to 20.0 C to determine if the remaining eggs would hatch.

Results. The results of this experiment are summarized in Table 2. The first group of eggs to hatch were those at 7.5 C. The lowest experimental temperature at which eggs hatched was 5.0 C. No eggs hatched at 2.5 C even after 30 days and these failed to hatch even after being returned to 20 C. Examination of these eggs showed that the embryos had died and dried up. There was a greater percentage hatch at 7.5 C (92.2%) than at 5.0 C (66.0%).

Table 2. The hatching threshold for eggs of *Mamestra configurata*.

	Temperature ° C								
	2.5			5.0			7.5		
Replicate Number	1	2	3	1	2	3	1	2	3
Number hatching per replicate of 50	0	0	0	31	33	35	47	44	48
Average percent hatching	0.0			66.0			92.2		

The developmental-hatching threshold. – The developmental-hatching threshold is the lowest temperature at which complete development from fertilization to eclosion can occur (Johnson, 1940). This threshold is the most important of those so far discussed, because, for eggs of some species, it can be used as an aid in determining distribution. Obviously, areas in which the daily high temperature is always below this threshold for a particular insect, will not have that insect present.

This experiment was designed to determine the lowest temperature at which complete development of eggs of *Mamestra configurata* could occur. Three different relative humidities were used to show if

humidity had any influence on development. Previous research had shown that complete embryogenesis could occur at 10.0 C but not at 5.0 C.

Methods. Eggs were collected over a period of three days from a culture of adults maintained at 15.0 ± 0.5 C and 60% RH. The methods used for collecting and handling eggs were identical to those described previously, with the exception that they were collected when less than 1 hour old to insure that little, if any, development had occurred.

For each daily collection, the eggs were divided into ten groups of 30, each group being placed in a 1 mm cap vial. One of the groups was placed at 20.0 ± 0.5 C and left for the remainder of the experiment as a test of egg viability. The remaining nine groups formed the first of three replicates. Each of the nine vials was placed under a different experimental condition. Vials were placed at temperatures of 6.5 ± 0.25 C, 7.5 ± 0.25 C, and 8.5 ± 0.5 C and at relative humidities of about 0%, 60% and 98% for each temperature. Temperatures were maintained in an incubator (6.5 C), in a refrigerated water bath (7.5 C) and in a growth chamber (8.5 C). Relative humidity was controlled in 6 mm cap vials using saturated salt solutions (P_2O_5 for 0%, $Na_2Cr_2O_7 \cdot H_2O$ for 60% and K_2SO_4 for 98%) (Winston and Bates, 1960).

Eggs were observed daily for sign of development. When embryos reached the black head capsule stage, observations were made every two hours.

Results. Percentage hatch for each control was 90% or greater. In the experimental groups, hatching occurred only at 8.5 C and 98% RH. Development to the black head capsule stage occurred in some individuals at 8.5 C and 60% RH and at 7.5 C and 98% RH. Dissection of a portion of these embryos several days later revealed no outward sign of structural disorder.

The high temperature developmental-hatching threshold. – *Mamestra configurata* has a reported geographic range that spans vastly different climatic regions extending from Keg River in northern Alberta (Philip, pers. obs.) to Mexico City, Mexico (King, 1928). Populations occurring in central and northern Alberta are exposed to cool springs, warm short summers, and long cold winters, their eggs experiencing temperatures ranging from 5.0 C to just above 30.0 C. However, in the southern part of its range, it is likely that eggs of *Mamestra configurata* are exposed to a much higher range of temperatures.

The purpose of this experiment was to determine the high temperature developmental-hatching threshold for eggs of *Mamestra configurata* and to find out whether eggs of the cold adapted populations of Alberta retain some resistance to high temperature (30 C and above).

Methods. This experiment was performed essentially like the previous ones, (developmental-hatching threshold) except that temperatures of 30.0 ± 0.5 C, 31.5 ± 0.5 C, 32.5 ± 0.5 C and 33.5 ± 0.5 C were used. Temperatures of 30.0 C and 35.5 C were maintained in a heated water bath and of 31.5 C and 32.5 C in incubators. Humidities were maintained using saturated salt solutions of P_2O_5 for 0% RH, NH_4NO_3 for approximately 60% RH and $K_2Cr_2O_7$ for 98% RH (Winston and Bates, 1960).

Results. The results of this experiment are summarized in Table 3. The listings are the totals of three replicates of 30 eggs. Unlike eggs in the previous experiment, relative humidity did not have a significant effect on hatching. Of the four temperatures tested, hatching occurred only at 30.0 C regardless of humidity. Some development occurred in eggs at all other experimental temperatures. All eggs (with the exception of some, probably infertile) developed the characteristic brown pigment of the equator and micropylar areas.

Eggs at 32.5 C developed to the point where larvae were clearly visible through the chorion, however, sclerotization and pigment deposition did not occur.

Table 3. High temperature developmental threshold of eggs of *Mamestra configurata* and effects on it by relative humidity.

Temperature in ° C	No. hatching (maximum 90)*		
	0% RH	60% RH	98% RH
30	84	82	84
31.5	0	0	0
32.5	0	0	0
33.5	0	0	0

*Figures = totals of three replicates of 30 eggs.

Effects of constant temperature and relative humidity on embryogenesis

Effects of exposure to constant temperature and relative humidities of 0%, 60% and 98% on developmental rate. – When dealing with an insect pest species, knowledge of the effects of climatic factors, particularly those of temperature on various stages of its life cycle is imperative if reliable predictions of outbreaks are to be made and if successful control procedures are to be implemented. The most accurate way of determining individual effects of various field conditions on a particular instar of an insect is to duplicate every possible combination of those conditions in the laboratory. This, however, is usually impossible to do or is too time consuming. The usual alternative (although it lacks the same degree of accuracy) is to use a range of constant temperatures, encompassing the range found in nature and to extrapolate from these results to development in the field.

Few authors have attempted to evaluate the effects of relative humidity acting in conjunction with constant temperatures on insect embryogenesis. This is rather surprising when one considers the effect relative humidity can have on development (Buxton, 1932; Ludwick, 1945; and Bursell, 1974). Since *Mamestra configurata* has a large geographic range (King, 1928), it is probably exposed to a considerable range of relative humidities. This experiment was conducted to determine the effects that relative humidity might have on embryogenesis under constant temperature conditions.

Methods. Ten different temperatures combined with three different relative humidities were used to determine the effect of temperature and relative humidity on embryogenesis. The lowest temperature used was 8.5 C (ie., the developmental-hatching threshold); the highest 30.0 C (ie., the high temperature developmental threshold). The remaining temperatures began at 10.0 C and increased at 2.5 C increments. Growth chambers were used to maintain the temperatures of 8.5 C, 12.5 C, 20.0 C, and 25.0 C, and incubators for the remainder. The temperature in each incubator was monitored and found to vary no more than ± 0.5 C when the door was closed. For most experiments, the doors were opened briefly, once a day, to check egg development. Temperatures returned to equilibrium in less than 30 minutes after the door was closed.

Dry P₂O₅ was used to provide 0% RH, and KNO₃ to provide 98% RH at all temperatures used. NaBr·2H₂O was used to approximate 60% RH for temperatures of 10.0 C, 12.5 C, 15.0 C, 17.5 C and 20.0 C, Na₂Cr₂O₇·H₂O for a temperature of 8.5 C and NH₄NO₃ for the remainder (Winston and Bates, 1960). The saturated salt solutions were prepared and placed at the desired temperature 30 days prior to being used to allow them to equilibrate. Humidities in the chambers were checked prior to, during and after the experiment and were always found to be within 6% of the desired humidity.

Eggs used in this experiment were collected as previously described from a culture of adults kept at 20.0 ± 0.5 C and 60% RH. Thirty eggs were placed in each vial. These vials were exposed to the

experimental conditions within one hour of collection. The experiment was replicated three times. Early in the experiment, it became apparent that insufficient numbers of eggs could be collected at any one time to complete a replicate for the temperature treatments. Instead, the eggs of each collection were used in replicating the three relative humidity treatments used at each temperature.

The eggs were examined once a day until they had reached the black head capsule stage at which time observations were recorded at two hour intervals until hatching was complete.

Results. Results of these experiments are summarized in Table 4 and Figures 1–3. Hatching occurred at all temperatures tested. Rate of development (the reciprocal of the total development time measured in hours) showed a strong positive correlation with temperature (correlation coefficients of 0.978, 0.989 and 0.982 were recorded for 0%, 60%, and 98% RH respectively). The fastest development occurred at 30.0 C- the slowest at 8.5 C.

Humidity had considerable effect on development. Development but no hatching occurred at 0% RH for temperatures of 12.5 C and lower, and at 8.5 C for 60% RH. Hatching always occurred first in those eggs at 98% RH followed by those at 60% RH and 0% RH.

Figures 1 to 3 demonstrate the effects of relative humidity and temperature on development. The straight lines (B) are drawn on the basis of the linear regression equation $Y = 7.43 + 1,966.44x$; $Y = 8.15 + 1,761.23x$ and $Y = 8.22 + 1,708.85x$ for 0%, 60% and 98% RH respectively. These lines are the velocity lines and represent the percentage of total development that occurs during one hour at that temperature. The points on and around these lines are the calculated values based on the reciprocal of the mean development time (listed in Table 4).

The hyperbolic curve (A) is based on the mean development time in hours at the experimental temperatures and humidities indicated. The squares on the graph represent the mean development time in hours for that temperature and humidity.

Effects of constant exposure to a temperature of 35.0 C on development of eggs of different ages. –

Results of preliminary experiments had suggested that *Mamestra configurata* is imperfectly adapted to the climatic regime found in the prairie provinces (Putnam, 1972). To perfectly adapt to this climate, the pupal population of *Mamestra configurata* should have an obligatory diapause (diapause development in this insect has been studied by Bailey (1976) and Bodnaryk (1978)). This however, does not always happen since flights of newly-emerged adults have been taken in blacklight traps in late fall, and some field-collected pupae have been shown to develop without exposure to cold (Philip, pers. comm.). These observations suggest that at least part of the population has either a facultative diapause or lacks it completely. The existence of this partial late second generation in the prairie provinces suggests that *Mamestra configurata* may be bi- or multivoltine in more southerly parts of its range.

The main purposes of this experiment were to determine if eggs of *Mamestra configurata* demonstrate a tolerance to high temperature and to discover the length of exposure required to produce 50 and 95% mortality. A temperature of 35.0 C was chosen for two reasons; because previous experiments had shown that this was above the upper developmental-hatching threshold and because temperatures of 35.0 C or greater for periods over 16 hours per day have been recorded in Arizona cotton fields by Fry and Surber (1971), well within *Mamestra configurata*'s range. Their study of the effects of high temperature on embryonic mortality included eggs of *Estigmene acrea*, a species often found in conjunction with *Mamestra configurata*, and which has a similar life cycle in Alberta (Beirne, 1971).

Methods. Eggs used in this experiment were collected from a culture of adults reared at 20.0 ± 0.5 C, as previously described.

Eggs of four different ages (3 hours, 24 hours, 48 hours, and 96 hours) were exposed to 35.0 C continuously for periods of 13, 20, 30, 45 and 67.5 hours. Six replicates of 20 eggs were used for each of the four different ages.

Table 4. Effect of temperature and three relative humidities on mean development time and development rate of eggs of *Mamestra configurata*.

Temperature °C	Mean development time in hours	Mean % development per hour
<u>0% RH**</u>		
8.5	x	x
10.0	x	x
12.5	x	x
15.0	259.70	0.00385
17.5	226.49	0.00441
20.0	143.28	0.00698
22.5	124.98	0.00800
25.0	108.13	0.00923
27.5	91.70	0.01090
30.0	87.97	0.01140
<u>60% RH**</u>		
8.5	x	x
10.0	576.19	0.00173
12.5	462.65	0.00216
15.0	252.32	0.00396
17.5	220.71	0.00453
20.0	135.14	0.00740
22.5	118.80	0.00842
25.0	100.92	0.00991
27.5	83.05	0.01200
30.0	78.71	0.01270
<u>98% RH**</u>		
8.5	879.70	0.00114
10.0	564.59	0.00177
12.5	458.39	0.00218
15.0	250.04	0.00399
17.5	218.88	0.00457
20.0	133.02	0.00752
22.5	116.75	0.00856
25.0	98.60	0.01010
27.5	81.13	0.01230
30.0	76.86	0.01300

(x — did not complete development to eclosion)

(** means of 3 replicates of 30 eggs per replicate)

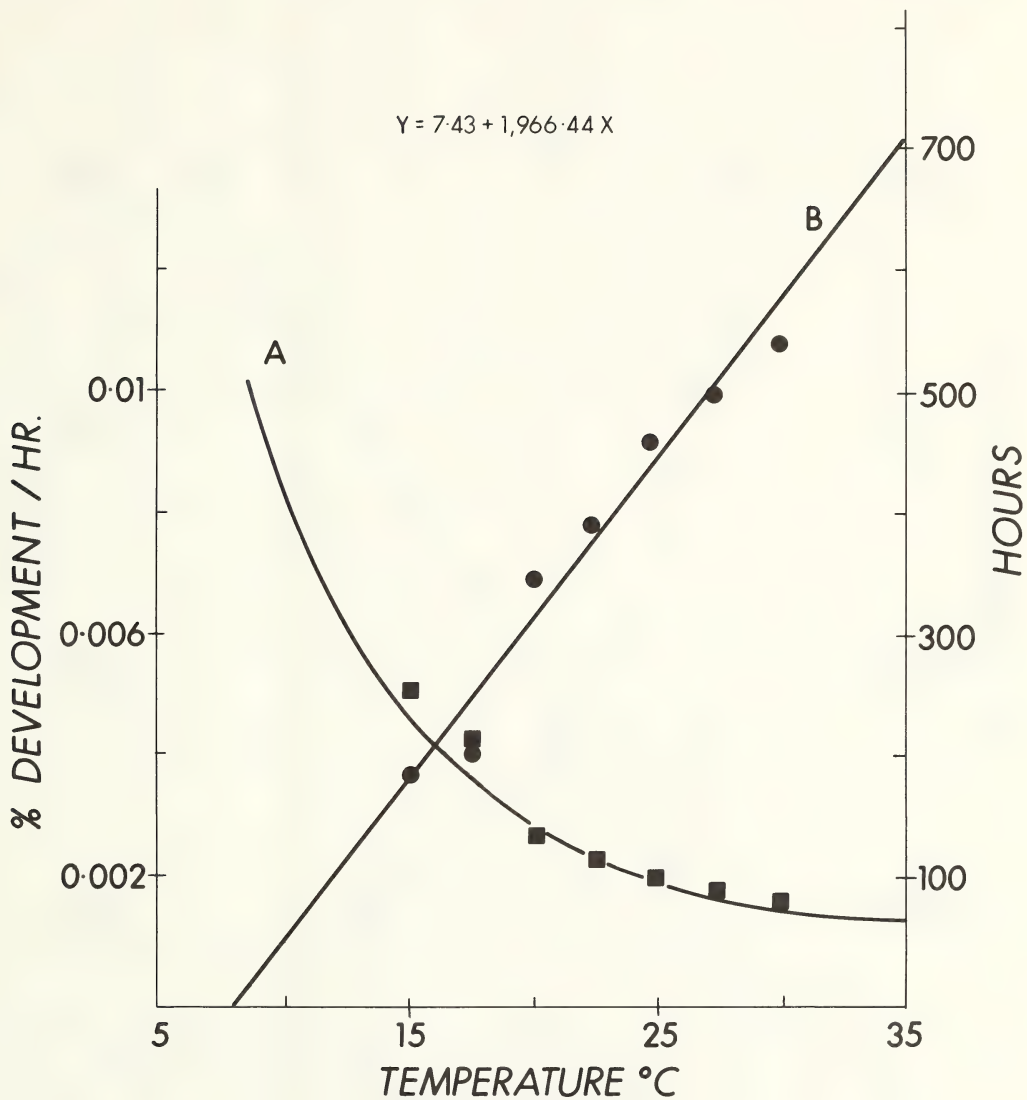


Figure 1. The developmental curve -A; and the velocity line-B; at 0% RH for embryogenesis of eggs of *Mamestra configurata*.

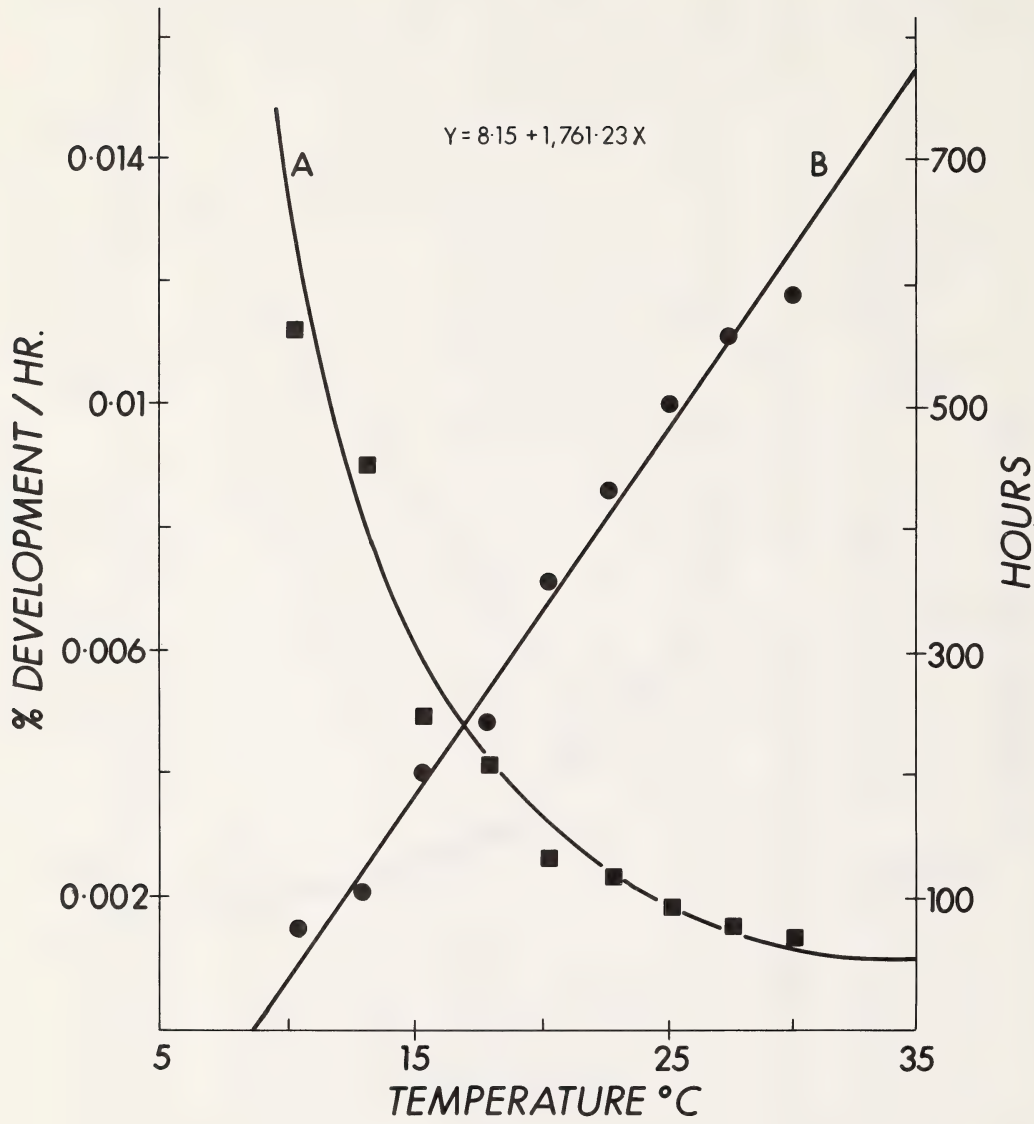


Figure 2. The developmental curve-A; and the velocity line-B; at 60% RH for embryogenesis of *Mamestra configurata*.

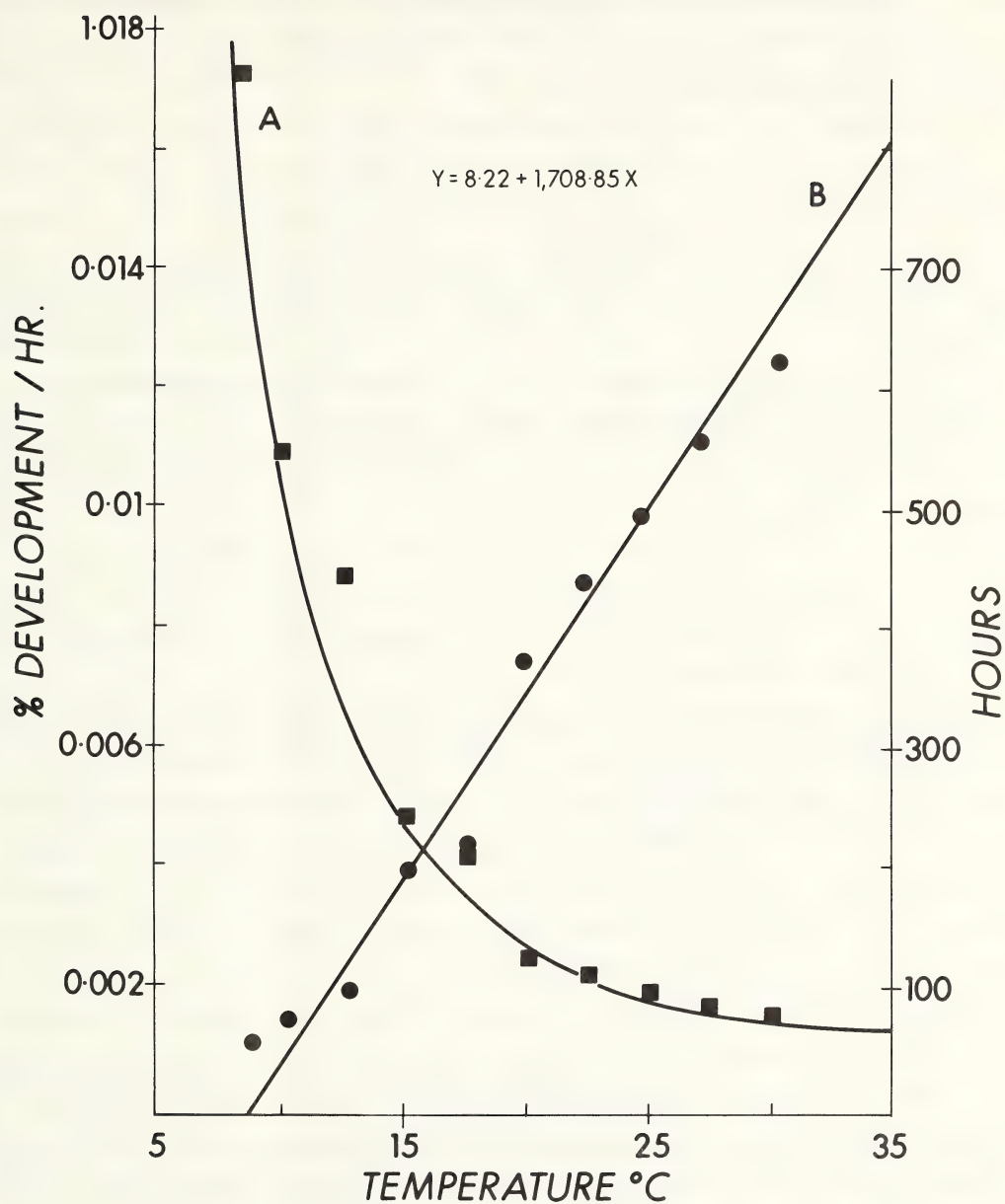


Figure 3. The developmental curve-A; and the velocity line-B; at 98% RH for embryogenesis of eggs of *Mamestra configurata*.

The eggs were collected daily when less than two hours old, divided into groups of six to form replicates, and the remaining vials were used as a check to determine natural mortality. Eggs that were to be used later were left at 20.0 ± 0.5 C and approximately 60% RH until they reached the desired age. When this occurred the eggs were placed in a 160 mm desiccator located in an incubator set at 35.0 C. The humidity in the desiccator was maintained at approximately 60% with a saturated salt solution of NH_4NO_3 (Winston and Bates, 1960).

The temperature in the incubator never varied more than 0.5 C. The temperature in the desiccator and within the vials was checked periodically and showed little variance (0.25 C) from that of the incubator. The incubator was opened only when it was necessary to place or remove vials.

Once the treatment was completed, the eggs in the vials were returned to 20.0 ± 0.5 C and 60% RH, and the tops of the vials were covered with plastic screening to prevent larval escape. The numbers hatching were recorded twice daily. Abbot's formula (Abbot, 1925) was used to determine the net percent mortality. Natural mortality was considered to be the highest mortality that was not a function of the treatment.

Variance analysis was used to determine the amount of variance caused by replication and error.

Results. The results of this experiment are summarized in Tables 5 to 8.

The mean time in hours required to produce 50% mortality were 34.45 ± 1.4 , 33.19 ± 3.49 , 32.8 ± 1.33 and 35.17 ± 1.11 for 3 hour, 24 hour, 48 hour and 96 hour old eggs respectively; and to produce 95% mortality were 51.27 ± 3.55 , 48.31 ± 3.34 , 50.03 ± 3.4 and 54.95 ± 4.14 for 3 hour, 24 hour, 48 hour and 96 hour old eggs respectively. From this data it can be concluded that exposures of greater than 37 hours to a temperature of 35.0 C will result in 50% or greater mortality and exposures of 60 hours will result in 95% or greater mortality, to eggs of *Mamestra configurata* regardless of their age.

Variance analysis and the resulting F-values showed that length of exposure was highly significant in determining mortality (Tables 5 to 8).

Effects of constant exposure to a temperature of 5.0 C on development of eggs of different ages. – When we began this research, we found that *Mamestra configurata* was difficult to rear continuously in the laboratory. Part of the problem was feeding the large number of larvae produced. The main purpose of this experiment was to determine the length of time eggs of *Mamestra configurata* could be stored at 5.0 C without causing excessive mortality. The temperature of 5.0 C was chosen for two reasons: (1) under natural conditions, eggs could be exposed to this temperature or lower (Average minimum temperature for July in rape growing areas in Central Alberta are: Stettler 10.2 C, Vermilion 9.6 C, Edmonton 9.1 C and Calgary 9.5 C (Philip, in note to Heming). Therefore, it is doubtful whether eggs would be exposed very long to temperatures of 5.0 C), and (2) 5.0 C is below the developmental-hatching threshold (8.5 C), but above the developmental threshold (between 0.0 and 2.0 C). A by-product of this research was to determine the length of exposure to 5.0 C required to produce 50% and 95% mortality.

Methods. Procedures used in this experiment were identical to those of the experiment with a constant temperature of 35.0 C, with the following exceptions: (1) the exposure was to 5 C; (2) $\text{NaBr} \cdot 2\text{H}_2\text{O}$ (Winston and Bates, 1960) was used to maintain approximately 60% RH, and (3) exposure times of 3, 45, 67, 101, 151, 227, 340, 510 and 765 hours were used. Additional times of 83, 189, 273 hours were used for eggs 48 hours old when initial mortality was high.

Probit analysis was used to transform sigmoidal dosage mortality curves into straight lines (Bliss, 1935). Variance analysis was used to determine the sources of variation and the effects of the treatment.

Results. Results of this experiment are summarized in Tables 9 to 12 and Figures 4 to 7.

Generally, resistance to cold appeared to increase as the age of the egg increased. Initial mortality occurred after 67 hours with 3 hour old eggs, after 151 hours with 24 hour old eggs, after 227 hours with

Table 5. Effect of continuous exposure to 35.0 C on three hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	13.0	0.00	
120	20.0	0.00	
120	30.0	32.35	4.5407
120	45.0	84.31	6.0069
120	67.5	100.00	

Treatment F-value 433.06 (F at 1% 4.43) with 4 DF

Between Treatment F-value 1.72 (F at 5% 2.71) with 20 DF

Mean number of hours of exposure at 35 C required to produce 50% and 95% mortality are: 34.45 ± 1.40 and 51.27 ± 3.55 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 6. Effect of continuous exposure to 35.0 C on 24 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	13.0	0.00	
120	20.0	0.00	
120	30.0	41.66	4.7895
120	45.0	84.26	6.0051
120	67.5	100.00	

Treatment F-value 404.1 (F at 1% level 4.43) with 4 DF

Between Treatment F-value 0.77 (F at 5% level 2.71) with 20 DF

Mean number of hours of exposure to 35 C required to produce 50% and 95% mortality are 33.19 ± 3.49 and 48.31 ± 3.34 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 7. Effect of continuous exposure to 35.0 C on 48 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	13.0	0.00	
120	20.0	0.00	
120	30.0	44.06	4.8516
120	45.0	87.28	6.1407
120	67.5	100.00	

Treatment F-value 805 (F at 1% level 4.43) with 4 DF

Between treatment F-value 0.82 (F at 5% level 2.71) with 20 DF

Mean number of hours of exposure to 35 C required to produce 50% and 95% mortality are 32.8 ± 1.33 and 50.03 ± 3.4 respectively. Variance analysis showed that variation in percentage was a function of treatment.

Table 8. Effect of continuous exposure to 35.0 C on 96 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	13.0	0.00	
120	20.0	0.00	
120	30.0	34.77	4.6093
120	45.0	76.97	5.7388
120	67.5	100.00	

Treatment F-value 426.78 (F at 1% level 4.43) with 4 DF

Between treatment F-value 0.05 (F at 5% level 2.71) with 20 DF

Mean number of hours of exposure to 35 C required to produce 50% and 95% mortality are 35.17 ± 1.11 and 54.95 ± 4.14 hours respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 9. Effect of continuous exposure to 5.0 C on three hour old eggs of *Mamestra configurata*.

No. of Individuals tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	30.0	0.00	
120	45.0	0.00	
120	67.5	1.96	2.92
120	83.0	39.20	4.59
120	101.0	74.00	5.64
120	151.0	100.00	

Treatment F-value 568.84 (F at 1% level 3.85) with 5 DF

Between Treatments F-value 2.44 (F at 5% level 2.6) with 25 DF

Mean number of hours of exposure to 5 C required to produce 50% and 95% mortality are 90.57 ± 2.32 and 118.85 ± 5.87 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 10. Effect of continuous exposure to 5.0 C on 24 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in hours	Net % Mortality	Empirical Probit
120	30.0	0.00	
120	45.0	0.00	
120	67.5	0.00	
120	101.0	0.00	
120	151.0	4.46	3.30
120	189.0	50.14	5.00
120	227.0	82.08	5.91
120	340.0	100.00	

Treatment F-value 733.5 (F at 1% level 3.7) with 7 DF

Between treatments 5.13 (F at 5% level 2.42) with 35 DF

Mean number of hours of exposure to 5 C required to produce 50% and 95% mortality are 193.06 ± 5.09 and 252.93 ± 13.14 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 11. Effect of continuous exposure to 5.0 C on 48 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in Hours	Net % Mortality	Empirical Probit
120	30.0	0.00	
120	45.0	0.00	
120	67.5	0.00	
120	101.0	0.00	
120	151.0	0.00	
120	227.0	11.40	3.700
120	273.0	52.63	5.706
120	340.0	79.82	5.834
120	510.0	100.00	

Treatment F-value 445.7 (F at 1% level 3.51) with 8 DF

Between treatments F-value 2.19 (F at 5% level 2.18) with 40 DF

Mean number of hours of exposure to 5 C required to produce 50% and 95% mortality are 271.64 ± 8.26 and 389.05 ± 17.82 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

Table 12. Effect of continuous exposure to 5.0 C on 96 hour old eggs of *Mamestra configurata*.

No. of Individuals Tested	Length of Treatment in Hours	Net % Mortality	Empirical Probit
120	30.0	0.00	
120	45.0	0.00	
120	67.5	0.00	
120	101.0	0.00	
120	151.0	4.75	3.3354
120	227.0	9.09	3.6654
120	340.0	53.20	5.0803
120	510.0	83.81	5.9463
120	765.0	100.00	

Treatment F-value 811.8 (F at 1% level 3.51) with 8 DF

Between treatments F-value 1.04 (F at 5% level 2.18) with 40 DF

Mean number of hours of exposure to 5 C required to produce 50% and 95% mortality are 337.29 ± 17.52 and 633.87 ± 55.77 respectively. Variance analysis showed that variation in percentage mortality was a function of treatment.

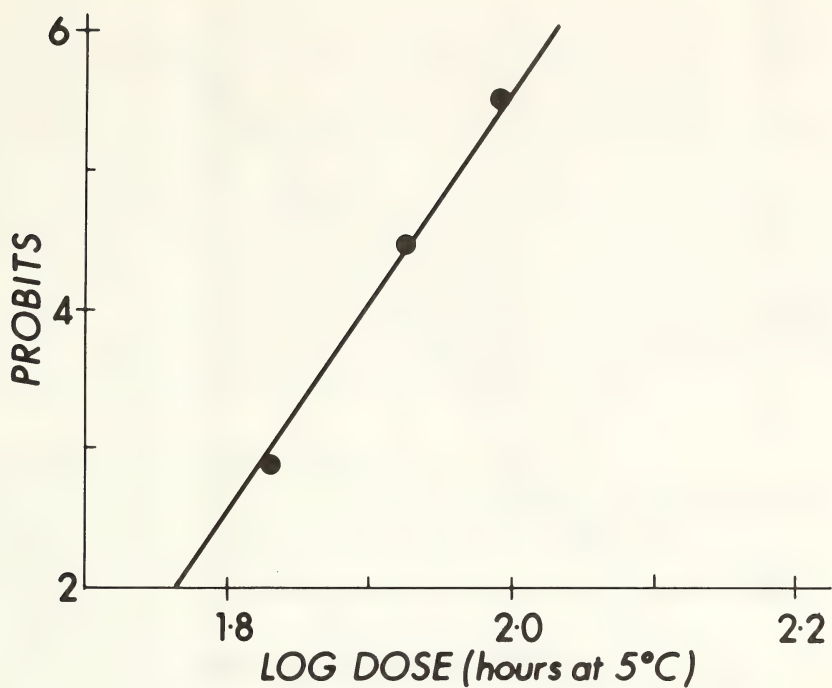


Figure 4. Probit regression line showing the effects of various dosages of 5.0 C on 3 hour old eggs of *Mamestra configurata*.

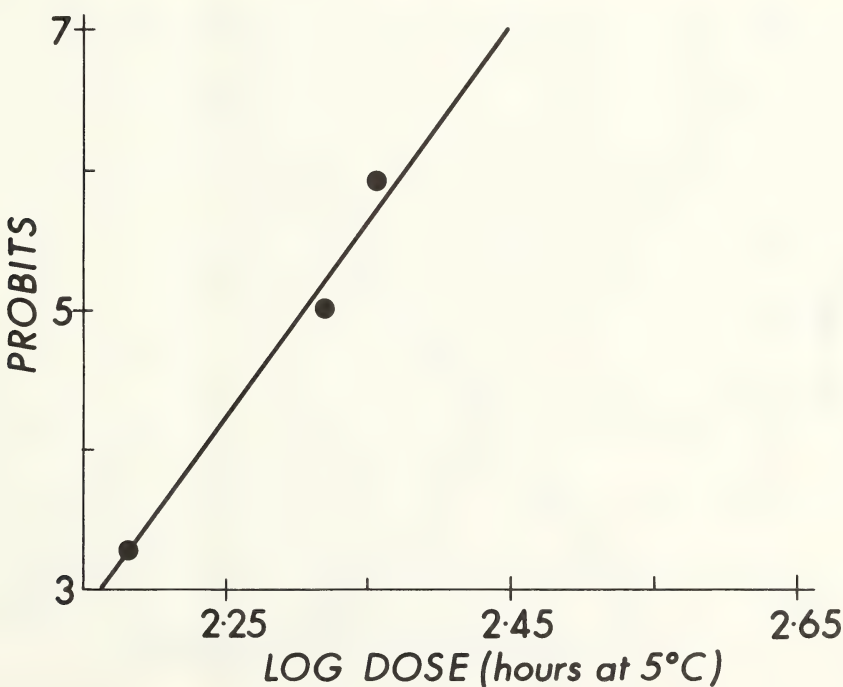


Figure 5. Probit regression line showing the effects of various dosages of 5.0 C on 24 old eggs of *Mamestra configurata*.

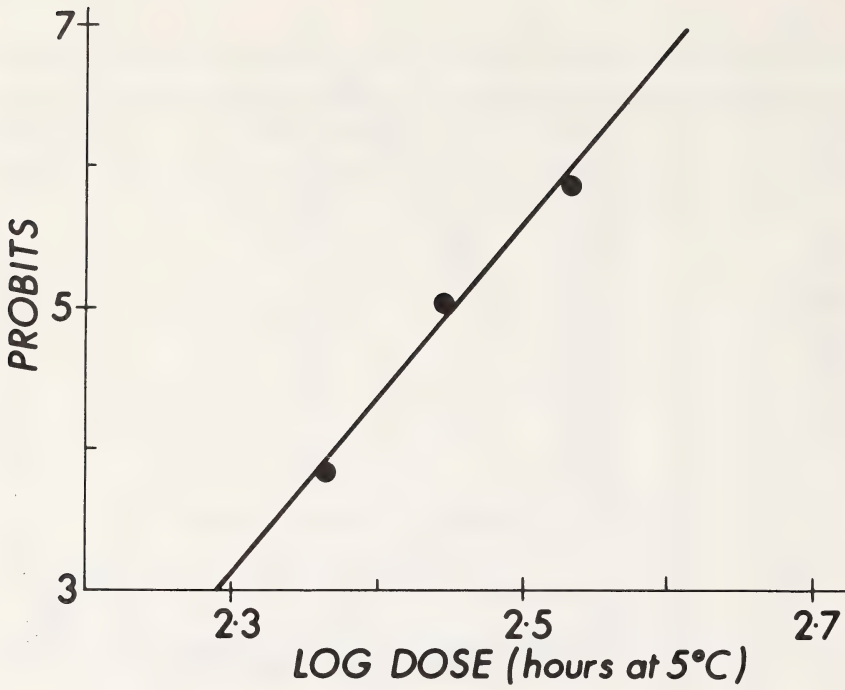


Figure 6. Probit regression line, showing the effects of various dosages of 5.0 C on 48 hour old eggs of *Mamestra configurata*.

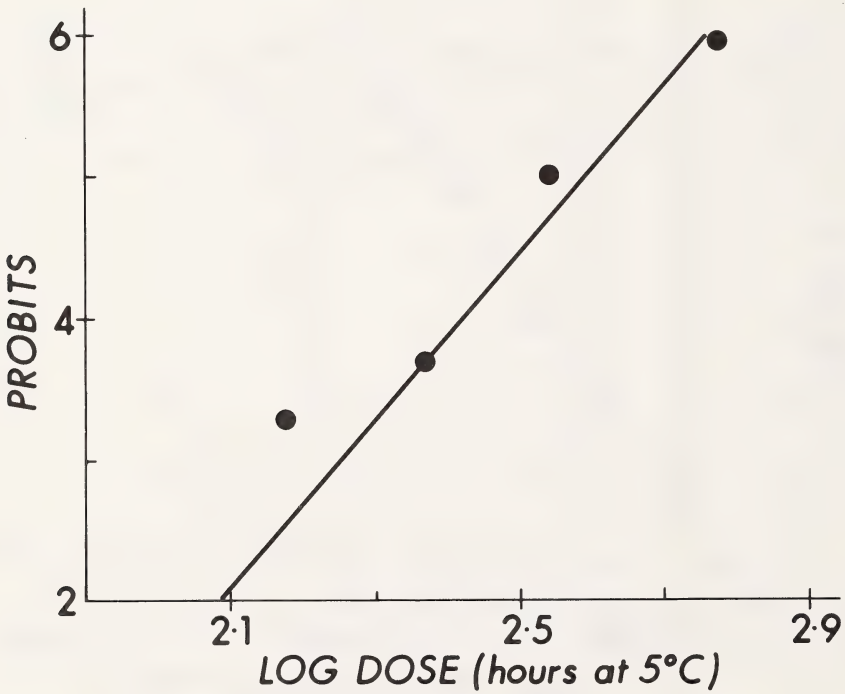


Figure 7. Probit regression line, showing the effects of various dosages of 5.0 C on 96 hour old eggs of *Mamestra configurata*.

48 hour old eggs and after 151 hours with 96 hour old eggs. However, after 227 hours the 48 hour old eggs suffered 11.4% mortality while, after time period, the 96 hour old eggs had only 9.1% mortality. The mortality difference is even greater after 340 hours exposure with 79.8% and 53.2% respectively for the 48 hour and 96 hour old eggs. Probably, there is a developmental age where exposure to 5.0 C is more critical than at other stages.

The increased resistance to cold is better illustrated when LD 50's and LD 95's are compared. Eggs 3 hours old had an LD 50 and an LD 95 of respectively 90.57 ± 2.32 hours and 118.85 ± 5.87 hours. These values for 24 hour old eggs were respectively 193.06 ± 5.09 hours and 252.93 ± 13.14 hours. Eggs aged 48 hours and 96 hours accrued 50% mortality after 271.64 ± 8.26 hours and 337.29 ± 17.52 hours and 95% mortality after 389.05 ± 17.82 hours and 633.87 ± 55.77 hours.

The F-values between error and treatment were highly significant (Tables 9–12), but variance between treatments was significant only for the 24 hour group.

Effects of alternating temperature on development

Alternating temperatures are used in biological temperature research to determine effects that cannot be ascertained using constant temperature alone. For example, under alternating temperatures, eggs of *Oncopeltus fasciatus* (Heteroptera) can complete embryogenesis at a mean temperature several degrees lower than the lowest constant temperature at which complete embryogenesis can occur (Lin *et al.* 1954).

During development, organisms are often subjected to extreme temperatures that would be fatal to them if they were maintained over long periods. Knowledge of the effects of alternating temperature on mortality and rate of development aids us in understanding naturally occurring temperatures effects on development.

Two experiments were conducted on eggs of *Mamestra configurata* to determine the effects of varying daily exposures to extreme temperatures on development rate. The first experiment was designed to determine the effects of daily exposure to 35.0 C on rate of development; the second had 5.0 C as the experimental temperature. In both experiments, the alternate temperature used was 20.0 C.

Effects of daily alternation between temperatures of 20.0 C and 35.0 C on eggs of different ages. – The main purpose of this experiment was to determine if eggs of the experimental population could withstand daily exposure to 35.0 C. In Alberta, the ovipositional period of females of *Mamestra configurata* extends from late June to mid-July so that its eggs would rarely be exposed to a temperature of 35.0 C. However, since *Mamestra configurata* is partially bi-voltine (i.e., it lacks either an obligatory or a facultative diapause in some members of its populations), its eggs may be expected to show partial resistance to daily temperatures of 35.0 C.

The other purpose of this experiment was to determine if alternation of temperature influenced development rate. Alternation of a high temperature with a moderate temperature often results in a decrease in the development rate of an insect compared with its performance at a constant temperature equal to the mean of the alternating temperatures (Johnson, 1940).

Methods. Eggs were collected from a culture reared at 20.0 ± 0.5 C and approximately 60% RH, divided into groups of 10 and each group was placed in a 1 mm cap vial.

Four groups of ten individuals were used at each of 13 experimental exposures (from 1 to 22.5 hours daily at 35.0 C; see Table 13 to 16 for details). Eggs of four different ages (3, 24, 48, and 96 hours) were used to determine the effect of age on tolerance to 35.0 C.

Eggs from any one collection period were divided into as many groups of ten as their number allowed, and the resulting groups were subdivided into units of four. Each of these units was then given daily exposure of 35 C. One vial from each collection was left at 20.0 ± 0.5 C to determine fertility.

During exposure, the vials were placed on a platform in a desiccator. A saturated salt solution of NH_4NO_3 was used to produce an RH of approximately 60% (Winston and Bates, 1960). First exposure to 35.0 ± 0.5 C was made immediately after the eggs had reached the desired age and was repeated at the same time each subsequent day until completion of the experiment. After exposure, the eggs were returned to 20.0 ± 0.5 C for the remainder of the day.

Eggs were observed daily until they reached the black head capsule stage at which time observations were made at two hour intervals. The number hatching and the total length of the development period for each egg was then recorded.

The mean hatching time for each exposure and the mean temperature for each group was determined. This allowed a comparison to be made between mean development time of eggs maintained at constant temperatures and those maintained under alternating temperatures.

Fry and Surber's (1971) experiment on the effects of exposure to 35.0 C and 40% RH on eggs of *Estigmene acrea* was used as a model.

Results. Results of the various treatments are summarized in Tables 13 to 16. In general, daily exposures of one hour did not result in significant change in development time (Daily exposures of 2.9 hours or greater resulted in a significant change in development time.) regardless of the number of exposures.

Table 13. Effect of daily exposure to 35.0 C on development in three hour old eggs of *Mamestra configurata*.

Number of Individuals tested	Daily exposure to 35 C (h)	Total exposure to 35 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	6.0	132.514 \pm 1.63 A*	**
40	1.3	7.8	132.375 \pm 2.30 A	**
40	1.7	10.2	130.32 \pm 1.65	0.005
40	2.2	13.2	129.33 \pm 2.70	0.001
40	2.9	17.4	126.00 \pm 2.27	0.001
40	3.7	20.4	124.82 \pm 1.89	0.001
40	4.8	24.0	123.4 \pm 0.45 B	0.001
40	6.2	31.0	123.15 \pm 2.64 B	0.001
40	8.0	40.0	122.52 \pm 2.82	0.001
40	10.4	52.0	121.33 \pm 2.44	0.001

Treatment F-value 114.08 (F at 1% level 2.32) with 9 DF

*means followed by the same letter (A or B) are not significantly different (based on Duncan's New Multiple Range Test).

**Not significant at the 5% level using T-tests. Variance analysis showed that the difference noticed in development times was a product of the various treatments.

Table 14. Effects of daily exposure to 35.0 C on development in 24 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 35 C (h)	Total exposure to 35 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	5.0	130.51 ± 1.88	**
40	1.3	6.0	130.16 ± 2.15	0.050
40	1.7	7.0	128.43 ± 2.06	0.001
40	2.2	11.0	127.51 ± 1.59	0.001
40	2.9	14.5	125.12 ± 1.75	0.001
40	3.7	15.0	123.92 ± 1.58	0.001
40	4.8	16.0	121.55 ± 2.17 A*	0.001
40	6.2	24.8	121.31 ± 1.95 A	0.001
40	8.0	32.0	120.14 ± 1.63	0.001
40	10.4	40.8	119.33 ± 2.00	0.001
40	13.5	54.0	117.82 ± 1.90	0.001

Treatment F-value 174.89 (F at 1% level 2.32) with 10 DF

*means followed by the same letter (A) are not significantly different (based on Duncan's New Multiple Range Test).

**not significant at the 5% level using T-tests. Variance analysis showed that the difference noticed in development times was a product of the various treatments.

Duncan's New Multiple Range Test was used to determine if individual treatments within each experimental group varied significantly from each other. The difference between exposures of one hour and 1.3 hour daily to 35.0 C was not significant in the 3 hour old groups. Non-significant differences were shown also between daily exposures to 4.8 and 6.2 hours for both the 3 hour and 24 hour old groups. Eggs 48 hours old showed no significant difference in development time for daily treatments of 2.9, 3.7, and 4.8 hours, nor between treatments of 4.8 and 6.2 hours and 1.7 and 2.2 hours. Eggs 96 hours old showed no significant difference in development time for daily treatments of 1.0, 1.3, 1.7 or 2.2 hours. No significant variation occurred between treatments of 3.7 and 4.8 or 8.0 and 10.4 hours.

Variance analysis was also used to determine if the variation noted in development times was due to treatment. The resulting values showed that the treatments were highly significant in this.

A comparison between development times observed under constant temperature and under equivalent alternating temperatures showed that development at constant temperatures of 22.5 and 25.0 C occurred more rapidly than at an equivalent temperature produced by daily alternation between 35.0 C and 20.0 C but more slowly at a constant temperature of 20.0 C (Table 17).

Our results were difficult to reconcile with those of Fry and Surber (1971). A single exposure to 35.0 C and 40% RH for 20 hours, resulted in only a 1.6% hatch of salt marsh caterpillar, *Estimene acrea*, eggs whereas all eggs of *Mamestra configurata* hatched that were given a similar exposure to 35.0 C and 60% RH for 22.8 hours. However, three exposures of 16 hours to 35.0 C and 40% RH resulted in 65.7% hatch for salt marsh caterpillar eggs while three similar exposures of 17.5 hours to 35.0 C and 60% RH resulted in only 27.5% hatch for *Mamestra configurata* eggs.

Table 15. Effects of daily exposure to 35.0 C on development of 48 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 35 C (h)	Total exposure to 35 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	4.0	129.94 ± 1.39	**
40	1.3	4.8	129.00 ± 1.63	**
40	1.7	5.6	128.32 ± 1.80 A*	0.05
40	2.2	8.8	128.15 ± 1.74 A	0.05
40	2.9	11.6	126.06 ± 1.64 B	0.001
40	3.7	12.0	125.78 ± 1.62 B	0.001
40	4.8	19.2	125.5 ± 1.54 B C	0.001
40	6.2	23.09	124.49 ± 1.28 C	0.001
40	8.0	28.05	124.05 ± 1.37	0.001
40	10.4	34.7	123.53 ± 1.43	0.001
40	13.5	42.5	122.0 ± 1.30	0.001
40	17.5	51.5	119.27 ± 1.35	0.001

Treatment F-value 105.36 (F at 1% level 2.32) with 11 DF

*means followed by the same letter (A,B,C) are not significantly different (based on Duncan's New Multiple Range Test).

**Not significant at the 5% level using T-test. Variance analysis showed that the difference noticed in development times was a product of the various treatments.

Effects of daily alternation between temperatures of 5.0 C and 20.0 C on eggs of different ages. – In the province of Alberta, *Mamestra configurata* has been recorded from almost all rape growing areas, a territory extending from south of Lethbridge to north of Keg River, a distance of about 966 km (Philip, pers comm.). Over much of this range, temperatures during the ovipositional period (June to July) could fall to 5.0 C or lower (i.e. below the developmental-hatching threshold, 8.5 C) for short periods (Canadian Department of Transport Meteorological Records, 1971–1974). The primary purpose of this experiment was to determine the effects of a varying exposure to 5.0 C on development time of eggs. A secondary purpose was to determine if alternation of temperatures would produce an acceleration in development over those of eggs maintained at a constant equivalent temperature.

Methods. Methods and materials used in this experiment were identical to those of the previous one except that (1) daily exposure was to 5 C, (2) the saturated salt solution used to maintain 60% RH was Na₂Cr₂O₇·H₂O, and (3) 25 rather than ten individuals were used in experiments involving three hour old eggs.

Results. The effects of the various treatments are summarized in Tables 18 to 21.

T-tests were used to determine the significance of the effect of treatment on development time. In all cases, the treatments produced a significant delay in development as compared with that of controls. Variance analysis was used to determine if the difference noted in development times was a function of treatment. In all cases, the difference noted between development times was highly significant at the 1% confidence level.

Duncan's New Multiple Range Test was used to determine if the individual treatments produced a significant difference in development times within individual test groups. In all cases, this test showed that the treatments differed at the 5% confidence level.

When the rates of development of eggs under constant temperature and under its alternate temperature equivalent were compared, those under the alternating temperatures developed more rapidly (Table 22).

Table 16. Effects on daily exposure to 35.0 C on development of 96 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 35 C (h)	Total exposure to 35 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	2.0	132.78 \pm 1.10A*	**
40	1.3	2.4	132.75 \pm 1.32A	**
40	1.7	3.4	132.58 \pm 1.06A	**
40	2.2	4.4	132.72 \pm 1.84A	**
40	2.9	5.8	132.058 \pm 1.87	0.050
40	3.7	6.0	131.62 \pm 1.82B	0.050
40	4.8	9.6	131.44 \pm 1.62B	0.001
40	6.2	12.4	130.91 \pm 1.66	0.001
40	8.0	16.0	130.00 \pm 1.61C	0.001
40	10.4	18.96	129.74 \pm 1.84C	0.001
40	13.5	21.29	128.56 \pm 1.40	0.001
40	17.5	29.89	127.79 \pm 1.53	0.001
40	22.5	28.89	126.39 \pm 1.41	0.001

Treatment F-value 56.39 (F at 1% level 2.32) with 12 DF

*means followed by the same letter (A,B,C) are not significantly different (based on Duncan's New Multiple Range Test).

**Not significant at the 5% level using T-tests.

Variance analysis showed that the difference noticed in development times was a product of the various treatments.

Table 17. Comparison of development rate in hours and in hour-degrees at constant temperature and at an equivalent alternating temperature (35.0 and 20.0 C) of eggs of *Mamestra configurata*.

Temperature C°	Development time in hours	
	Constant	Alternating
20.0	135.14 (2703)*	132.16 (2643)
22.5	118.8 (2673)	121.55 (2735)
25.0	100.92 (2523)	119.33 (2983)

*Numbers in brackets are equivalent development rates in hour-degrees.

Table 18. Effects of daily exposure to 5.0 C on development in three hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 5 C (h)	Total exposure to 5 C ¹ (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
100	1.0	6.0	137.54 ± 1.99	0.001**
100	1.3	7.8	138.76 ± 1.84	0.001
100	1.7	10.2	142.08 ± 2.11	0.001
100	2.2	13.2	141.12 ± 1.74	0.001
100	2.9	17.4	142.31 ± 1.83	0.001
100	3.7	25.9	156.51 ± 2.00	0.001
100	4.8	33.6	163.91 ± 1.34	0.001
100	6.2	49.6	180.79 ± 1.57	0.001
100	8.0	64.0	194.76 ± 1.74	0.001
100	10.4	102.5	233.92 ± 1.65	0.001
100	13.5	162.0	289.93 ± 2.11	0.001
100	17.5	332.5	454.20 ± 1.78	0.001

Treatment F-value 550 (F at 1% level 2.32) with 11 DF

**level of significance comparing mean development times of the combined replicates and the control group using T-tests.

The difference in development times between treatments was analysed by variance analysis and was found to be highly significant and, almost completely, a function of treatment.

Table 19. Effects of daily exposure to 5.0 C on development in 24 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 5 C (h)	Total exposure to 5 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	5.0	135.45 ± 0.997	0.001**
40	1.3	6.5	138.50 ± 1.66	0.001
40	1.7	8.5	140.29 ± 1.78	0.001
40	2.2	11.0	141.16 ± 1.61	0.001
40	2.9	14.5	145.83 ± 1.54	0.001
40	3.7	22.2	151.25 ± 2.81	0.001
40	4.8	28.2	160.96 ± 1.35	0.001
40	6.2	37.2	173.07 ± 1.73	0.001
40	8.0	56.0	183.61 ± 1.74	0.001
40	10.4	93.6	230.69 ± 1.76	0.001
40	13.5	136.0	258.5 ± 1.34	0.001
40	17.5	262.5	387.22 ± 1.53	0.001

(continued on page 283)

Table 19. (Continued)

Treatment F-value 63,708 (F at 1% level 2.32) with 11 DF

**level of significance comparing mean development times of the combined replicates and the control group using T-tests.

The difference in development time between treatments was analyzed using variance and found to be highly significant and, almost completely, a function of treatment.

Table 20. Effects of daily exposure to 5.0 C on development in 48 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 5 C (h)	Total exposure to 5 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	4.0	138.95 \pm 1.90	0.001**
40	1.3	5.2	140.38 \pm 1.50	0.001
40	1.7	6.8	142.95 \pm 2.01	0.001
40	2.2	8.8	144.82 \pm 1.57	0.001
40	2.9	14.5	149.78 \pm 1.64	0.001
40	3.7	18.5	155.19 \pm 1.91	0.001
40	4.8	24.0	159.66 \pm 1.49	0.001
40	6.2	31.0	165.94 \pm 1.82	0.001
40	8.0	40.0	176.03 \pm 1.46	0.001
40	10.4	62.4	194.72 \pm 1.73	0.001
40	13.5	108.0	236.61 \pm 1.84	0.001
40	17.5	210.0	339.41 \pm 1.52	0.001

Treatment F-value 39,499 (F at 1% level 2.32) with 11 DF

**level of significance comparing mean development times of the combined replicates and the control group using T-tests.

The difference in development time between treatments was analyzed using variance analysis and was found to be highly significant and, almost completely, a function of treatment.

Table 21. Effects of daily exposure to 5.0 C on development of 96 hour old eggs of *Mamestra configurata*.

Number of individuals tested	Daily exposure to 5 C (h)	Total exposure to 5 C (h)	Mean development time of combined replicates (h)	Significance between control hatching time & combined replicates
40	1.0	2.0	133.83 ± 1.68	0.001**
40	1.3	2.6	135.91 ± 1.74	0.001
40	1.7	2.4	137.03 ± 1.67 A*	0.001
40	2.2	4.4	137.18 ± 1.31 A	0.001
40	2.9	5.6	138.67 ± 1.63	0.001
40	3.7	7.6	140.43 ± 2.71	0.001
40	4.8	9.6	141.84 ± 1.11	0.001
40	6.2	12.4	145.20 ± 1.95	0.001
40	8.0	24.0	156.65 ± 1.81	0.001
40	10.4	31.2	162.17 ± 1.81	0.001
40	13.5	54.0	184.94 ± 1.72	0.001
40	17.5	87.5	219.37 ± 1.66	0.001
40	22.5	308.5	435.33 ± 1.91	0.001

Treatment F-value 78,120 (F at 1% level 2.18) with 12 DF
*means followed by the same letter (A) are not significantly different based on Duncan's New Multiple Range Test.
**level of significance comparing mean development times of the combined replicates and the control group using T-tests.
The difference in development times between treatments was analysed using variance analysis and was found to be highly significant and, almost completely, a function of treatment.

Table 22. Comparison of development rate in hours and in hour degrees at constant temperature and at an equivalent alternating temperature (5 and 20 C) of eggs of *Mamestra configurata*.

Temperature C °	Development time in hours	
	Constant	Alternating
17.5	220.71 (3862)*	156.5 (2739)
15.0	252.32 (3785)	194.76 (2921)
12.5	462.65 (5783)	387.22 (4840)

*Numbers in brackets are equivalent development rates in hour-degrees.

DISCUSSION AND CONCLUSIONS

Temperature thresholds for embryogenesis

Study of temperature effects on organisms began when Reamur (1735, see Belehradek, 1930) recognized that a relationship exists between temperature and the activity of an animal. Since then, these relationships have been examined by numerous authors and reviewed by Crozier (1926), Belehradek (1930), Uvarov (1931), Janisch (1932), Howe (1967), Bursell (1974) and several others. The results of these studies led to the development of the concept of various temperature thresholds for developmental stages.

These are two principal types of temperature threshold; low temperature thresholds involving temperatures too low for certain developmental processes to be completed, and high temperature thresholds which consider temperatures too high for normal development. Determination of these thresholds, in embryogenesis, has been made primarily of the first type, probably because of the larger temperature coefficients existing between the various thresholds at lower temperatures.

Presently, four low temperature thresholds are recognized as affecting embryogenesis. Peairs (1927) defined the *developmental threshold* as "the temperature at which, on the descending scale, development ceases, and at which, on the ascending scale development is initiated". Johnson (1940) introduced the *hatching threshold* and the *developmental-hatching threshold* which are respectively, the lowest temperature at which hatching of a fully developed larva can occur, and the lowest temperature at which complete development from fertilization to eclosion can occur. The *hatching-survival threshold* was suggested by Hodson and Al Rawy (1956) and they chose Allee *et al.*'s (1949) definition of the "lowest temperature at which a given stage in the life history can be carried through to completion" for a definition.

The only high temperature threshold recognized for embryogenesis is the high temperature equivalent of the developmental-hatching threshold. It has also been suggested that there exists a high temperature threshold equivalent of the developmental threshold, but Uvarov (1931) questioned whether this temperature is distinct from the upper lethal temperature. He further stated that if there was an appreciable difference in temperature between the upper lethal point and the upper developmental threshold, then there should be a quiescent stage similar to the quiescence observed at temperatures below the developmental threshold but above the lower lethal point. This stage, referred to as *heat stupor*, has been recognized in relation to activity but, as yet has not been described for development. Theoretically, this stage could exist, although the range between it and the upper lethal temperature may be so restricted that its discovery will be of limited practical value.

The concept of the developmental threshold of Peairs (1927), has been given numerous names by various authors in attempts to convey with greater clarity the process that occurs at that particular temperature. It has been called "the critical point", "physiological zero" and "the minimum effective temperature" (Uvarov, 1931). More recent authors (e.g. Lin *et al.*, 1954) have chosen to ignore the original definition of this threshold and have used instead Johnson's (1940) developmental-hatching threshold definition as if it were synonymous. The developmental threshold is seldom determined analytically, but is generally arrived at by extrapolation from temperature and rate of development curves. This method assumes that the effects of temperature on duration of embryogenesis can best be represented, mathematically, by a hyperbolic function (Sanderson and Peairs, 1914). This function, when transformed into its reciprocal, produces a straight line. This line is often called the "velocity line", and represents the effects of temperature on rate of development. When plotted on a graph, the point

where the velocity line intercepts the temperature axis is the hypothetical zero of the hyperbola or the developmental threshold. This method is used extensively to derive the developmental threshold; for example it is 11.5 C for the corn earworm, *Heliothis zea* (Boddie), (Luckmann, 1963) and 11.0 C for the European corn borer *Ostrinia nubilalis* (Hubner) (Matteson and Decker, 1965).

The difficulty in using a straight line to describe rate of development was first pointed out by Krogh (1914) and later by Shelford (1927) and Peairs (1927). Peairs noted that the development rate deviated from a straight line near the extremes of the temperature range. Thus, thresholds determined using this method were higher than the actual threshold.

Johnson (1940) emphasized the need for determining thresholds empirically and the necessity of recognizing different thresholds for various stages of embryogenesis. He suggested that because there are distinct stages in embryogenesis, there should also be equally distinct temperature thresholds for development of these stages. He suggested that both hatching and developmental hatching thresholds be used. However, with the exception of a study on eggs of the milkweed bug *Oncopeltus fasciatus* (Dallas) (which showed them to hatch at a temperature 2.0 C lower than their developmental-hatching threshold if 90% of the previous embryonic development occurred at 20.0 C (Lin *et al.*, 1954)) most researchers have chosen to disregard both the hatching and the development-hatching thresholds.

The hatching survival threshold of Hodson and Al Rawy (1956) has also been ignored by recent workers, probably because of the extensive amount of time required for rearing immatures through to adulthood.

The *upper temperature developmental limit* can be considered to be the upper equivalent of the developmental-hatching threshold or the highest temperature at which complete development and eclosion can occur. This upper threshold has been described in representative species of many orders of insects, e.g. (Collembola) *Onychiurus furciferus* (Borner) (Choudhuri, 1960); (Hemiptera) (*Geocoris atricolour* Montd. (Dunbar and Bacon, 1927); (Diptera) *Phormia regina* Meig. (Melvin, 1934); (Coleoptera) *Epilachna corrupta* Mulsant (Pyenson and Sweetman, 1931); and (Lepidoptera) *Telea polyphemus* Cramer (Ludwick and Anderson, 1942). Bursell (1974) listed the upper limit for various insect species, the highest, 40.0 C, being recorded for *Ptinus tectus* Boield; the lowest, 28.0 C, for *Tribolium confusum* (Herbst), both Coleoptera.

The various temperature thresholds demonstrated for embryogenesis in eggs of *Mamestra configurata* show that these are well adapted to Alberta climatic conditions occurring at the time of oviposition. Some development occurs at temperatures as low as 2.0 C and fully developed eggs can hatch at temperatures as low as 5.0 C (3.5 C below the developmental-hatching threshold). Eggs can develop completely and hatch at temperatures ranging from 8.5 C to 30.0 C, temperatures similar to those recorded by Bailey (1976) for eggs of this insect. However, mortality at the developmental-hatching threshold (8.5 C) is high (77.8%). Normal temperatures (mean, maximum and minimum) for the ovipositional period rarely fall outside this developmental range (Department of Transport Meteorological Records).

Similar high mortality at the development-hatching threshold has been demonstrated for eggs of *Oncopeltus fasciatus* by Richards and Suannaksa (1962). It is probable that the larvae that hatched would not have reached maturity. Their hatching behaviour showed the same anomalies as those reported by Lin *et al.* (1954) for nymphs of *Oncopeltus fasciatus*. They found that even if these nymphs were transferred to ideal conditions, very few reached maturity. Larvae hatching under these conditions appear debilitated and have difficulty moving effectively. It is possible that these larvae have internal structural defects that result in early death.

The upper developmental-hatching threshold for eggs of *Mamestra configurata* recorded here (between 30.0 C and 31.5 C) is comparable to the 32.0 C value given by Bailey (1976) for eggs of this

species and resembles that of eggs of the armyworm, *Pseudaletia unipuncta* (Howe) (Guppy, 1969). He found that the rate of development for eggs of this species began to decrease when temperature was increased above 29.0 C. Eggs of *Mamestra configurata* probably follow a similar course of development. The lack of data supporting this belief probably arises from experimental error. Sample sizes (50 individuals) may have been too small to reveal the small percentage of individuals that might have hatched at temperatures above 30.0 C. Also, the interval between 30.0 C and the next temperature (31.5 C) might have been too large. Mortality in insects increases rapidly as temperature increases above their optimum temperatures (Stinner *et al.* 1974). Even if complete development is curtailed by temperatures in excess of 30.0 C, the occurrence of these temperatures in Western Canada during the incubation period is rare and would have little effect on development.

Effects of constant temperature and relative humidity on embryogenesis

Research conducted on the effects of temperature on insect embryogenesis can be broadly classed into two groups. The first treats the effects of constant temperature (often applied at different relative humidities); the second, the effects of alternating or varying temperatures on embryonic development. This subject has been reviewed by Sanderson (1910), Uvarov (1931), Janisch (1932), Howe (1967) and Bursell (1974). The effects of relative humidity have been reviewed by Buxton (1932) and Ludwick (1945).

One of the principal reasons that the effects of constant temperature on insect development are studied is the hope that the resulting developmental curves can be used to predict insect development in the field. Numerous attempts have been made to derive a general mathematical function or equation that describes the relationship between temperature and development in insects. These attempts have been reviewed by Crozier (1926), Uvarov (1931), Janisch (1932), Davidson (1944), and Howe (1967). The more widely used of these concepts are: day-degrees; thermal summation and summation of development units.

Improper use of these concepts often leads to grossly inaccurate results. This occurs when fluctuating temperatures are assessed in terms of a simple average rather than weighted according to the effects of each individual temperature on development (Bursell, 1974). The inaccuracy of these concepts arises from the assumption that the best way to represent mathematically the effect of temperature on rate of development, is through use of a straight line. Near the extremes of the temperature range for a species, the rate of development deviates from a simple linear relationship. At the lower extreme, the rate of development declines more slowly; at the upper extreme, more rapidly than would be expected from a strictly linear relationship. The resulting temperature and rate of development curve is thus closer to being sigmoidal than linear. However, when the temperature range between the maximum rate of development and the upper lethal limit is slight, the resulting curve is J-shaped (Howe, 1967).

Relative humidity can apparently have no effect on insect embryogenesis; or it can cause changes in development time, and influence mortality rates and developmental thresholds. These effects and others on invertebrates have been reviewed by Buxton (1932) and Ludwick (1945).

The rate of embryogenesis in eggs of *Mamestra configurata* showed a strong linear relationship with temperature over the range of temperatures used in this experiment. Deviation from this relationship occurred only at temperatures of 10.0 C and lower. Complete development and hatching occurred at temperatures ranging from 8.5 C to 30.0 C.

Low humidity retarded development regardless of temperature. It is possible that eggs of *Mamestra configurata* normally absorb from the atmosphere at least a portion of the water used during development. Extremely low humidity would inhibit this absorption and force development to rely upon already present reserves, thus slowing down rate of development.

Lower temperatures prolonged exposure to low humidities and resulted in increased mortality. Possible causes for this are (1) death due to desiccation as the eggs had insufficient water to complete development, (2) weakening of larvae through water loss, making the act of hatching more difficult, and (3) hardening of the chorion caused by desiccation, inhibiting hatching, or (4) by a combination of these factors.

The fastest rate of development always occurred at 98% RH followed by 60% RH and 0% RH. This suggests that eggs of *Mamestra configurata* absorb water during development and that water may become the limiting factor during some part of embryogenesis. Water absorption would be facilitated most in high humidity, and would decrease as humidity declines. It is unfortunate that we failed to monitor micro-climatic conditions within blossoming rape fields since such data would have facilitated speculation of this kind.

Effects of exposure to constant temperature and relative humidities of 0%, 60% and 90% on developmental rate. – In general, low relative humidity retards rate of development in insect eggs. We have shown this to be true too for eggs of *Mamestra configurata*. Regardless of the temperature used, hatching always occurred first at 98% RH followed by 60% and 0%. Relative humidity appeared to be more important in the lower temperature range (15.0 to 8.5 C). At 0% RH, hatching was inhibited at temperatures below 15.0 C. At the developmental-hatching threshold (8.5 C) hatching occurred only at 98% RH.

Bailey (1976) reared eggs of *Mamestra configurata* at 75% RH and at temperatures of from 6.0 to 36.0 C and found the time for completion of embryogenesis and hatching to decrease from 28 days at 8.0 C to 3 days at 28.0 and 32.0 C. These figures are similar to those recorded here: 36.6 days at 8.5 C and 98% RH, 3.2 days at 30.0 C and 98% and 3.3 days at 30.0 C and 60% RH (Table 4). These results agree with those reported for other Lepidoptera (Ludwick and Anderson, 1942).

Evidence from our experiments to suggest that both mechanical and physiological barriers retard and reduce hatching is that the number of individuals first to eclose at each of the humidities used remained relatively constant regardless of temperature. Differences of eight to ten hours occurred in eggs exposed to RH's of 0% and 98%. This evidence also suggests that the larvae were weakened and thus took longer to hatch. There is also evidence suggesting a physiological delay. Eggs exposed to 0% RH always required a longer time to develop brown pigmentation than did those exposed to higher humidities. This suggests that early stages of development are impaired by lack of access to atmospheric moisture. In many insects, development is enhanced by absorption of atmospheric moisture through a hydropyle (Wigglesworth, 1972). Although examination of eggs of *Mamestra configurata* failed to locate a similar structure, the numerous aeropyles present in the chorion could act in a similar capacity (Jones, 1979).

The experiments we conducted were not designed to determine the mechanism by which humidity affects development. Experiments using a greater range of humidities and tests of egg shell tensile strength would aid in determining which of physiological or mechanical barriers have the greater effect on mortality and rate of development.

Effects of constant exposure to a temperature of 35.0 C on development of eggs of different ages. – Constant exposure of eggs to 35.0 C produced approximately 50% mortality after 37 hours and 95% mortality after 20 hours regardless of egg age. (Tables 5–8). Comparison of the 50% and 95% mortality times of eggs of different ages demonstrated that older eggs had slightly more tolerance than their younger counterparts. However, the difference was slight and only much larger sample sizes and a greater number of exposures would demonstrate if the difference is significant.

Sensitivity to high temperature decreased in eggs of the silkworm *Bombyx mori* L., after meiosis but before syngamy (Ostryakova-Varshaver, 1958). The exact cause of death in these eggs at high temperatures was unknown. Denaturing of proteins, an upset in the balance of one or more metabolic

processes leading to accumulation of some toxic product of metabolism more quickly than it can be removed, desiccation, or starvation have all been suggested as contributing to heat death (Bursell 1974). It is possible that older eggs of *Mamestra configurata*, i.e. those 24, 48, and 96 hour old, might have shown greater resistance to heat if they had been kept at 30.0 C prior to testing them at 35.0 C. For example, eggs of *Drosophila* spp., show considerable variation in survival time depending upon the temperature at which the flies were reared. Rearing at 25.0 C more than doubled their survival time at 33.5 C compared with that of counterparts reared at 15.0 C (Chapman, 1971).

Two types of acclimation have been demonstrated in insects: a longlasting "developmental" acclimation and a transitory "physiological" one (Bursell, 1974). The first of these depends upon the temperature at which the insect was raised prior to treatment. Insects raised at higher temperature require a longer exposure to a particular high temperature to produce mortality than do their counterparts raised at a lower temperature. This acclimation appears to be permanent and is not affected by exposure to lower temperatures. Physiological acclimation, is readily reversible, its effectiveness being a function of both the temperature and length of exposure experienced prior to exposure to the experimental temperature (Bursell, 1974). For example, in one insect, the chalcid parasite *Dahlbominus fuscipennis* (Zett.) Baldwin and Riodin (1956) (in Bursell, 1974) found that the greatest amount of acclimation occurred after two hours exposure and declined to insignificant levels in the next 12 hours.

Effects of constant exposure to a temperature of 5.0 C on development of eggs of different ages. – Constant exposure of eggs of *Mamestra configurata* to 5.0 C had varying results (Tables 9–12). Resistance to cold increased with increasing age, suggesting that early stages of embryogenesis are more sensitive to low temperature. Thus, such stages may require daily exposure to favourable temperature before they can complete development (Lin *et al.*, 1954). Two day old eggs of the cabbage looper, *Trichoplusia ni* exposed to 11.0 C showed increased mortality compared to that of one or three day old eggs (Kishabo and Henneberry, 1966).

Death of embryos at low temperature may result from structural abnormality. For example, some embryos of *Bombyx mori*, stored at low temperatures, showed the following abnormalities: the amniotic cavity was larger than normal and was broken in some individuals. Others showed incomplete dorsal closure, resulting in parts of the alimentary canal being left outside the body (Totani, 1960). It thus appears that constant exposure to low temperature can disrupt metabolism and subsequent development of the embryo.

Another cause of death caused by continuous exposure to low temperature may be a lack of sufficient food reserves to allow for complete development once the eggs are returned to a favourable temperature (Richards, 1964). This does not appear to be the cause of death for three hour old eggs of *Mamestra configurata* since none of these showed any deposition of pigment (a sign that they had not developed significantly at the end of treatment). As in the previous experiment different results would have occurred if the eggs had been pre-conditioned prior to exposure to the experimental temperature.

Effects of alternating temperature on development

Research on the effects of alternating temperature on insect embryogenesis are of the following types: (1) a low temperature is alternated with a medial temperature (medial temperatures are a range of temperatures for an insect species, where the rate of development most closely approaches a linear relationship with temperature), (2) a high is alternated with a medial, (3) two medial temperatures are alternated with each other, or (4) a temperature series based on field conditions is used to simulate natural conditions.

These effects have been reviewed by Uvarov (1931), Howe (1967), Wigglesworth (1972) and others.

In general, such treatment can (1) accelerate development rate, (2) decrease development rate, (3) influence the developmental-hatching threshold, (4) influence mortality, or (5) have no effects.

Exposure to alternating temperatures appeared to either increase or decrease development rate in eggs of *Mamestra configurata* depending on the situation. Alternation between 5.0 C and 20.0 C apparently accelerated development compared with that of eggs experiencing an equivalent constant temperature whereas alternation between 20.0 C and 35.0 C seemed to decrease development rate.

Effect of daily alternation between temperatures of 20.0 C and 35.0 C on eggs of different ages. – Eggs of *Mamestra configurata* demonstrated an increasing tolerance to longer daily exposures to 35.0 C as they matured (Tables 13–16). Eggs two days old at the beginning of the treatments withstood longer daily exposures than did younger eggs. However, this does not mean that they showed a greater overall resistance to temperatures of 35.0 C. When the total time spent at 35.0 C is compared, it shows that regardless of age no eggs hatched from any group exposed to more than 55 hours. This data, combined with that of the experiment on constant exposure to 35.0 C (Tables 5–8) suggest that the effects of 35.0 C may be cumulative. If this is true, it is unlikely that any one stage of embryogenesis is the most susceptible. Rather, it suggests that the whole of metabolism is disrupted, perhaps leading to a build up of toxic materials which, in turn, causes death (Bursell, 1974).

The time required for complete development was greater under alternating than under constant temperature (Table 17). This agrees with similar results recorded for eggs of the Japanese beetle, *Popillia japonica* by Ludwick (1938), for those of *Drosophila melanogaster* Meigen by Ludwick and Cable (1933) and for those of other fruit flies by Messenger and Flitters (1958). The reason for this is the sigmoidal nature of the temperature and rate of development curves. Above the optimum temperature (30.0 C for eggs of *Mamestra configurata*), rate of development begins to decline, this decline increasing rapidly as temperature increases. Thus, the actual rate of development at 35.0 C is probably similar to that occurring at 30.0 C or lower. This means that the time spent at 35.0 C is equivalent to an identical time spent at 30.0 C and that this should be calculated on this basis rather than on a hypothetical linear relationship supposedly existing between temperature and development curves. If the actual sigmoidal relationship is used, neither a retardation nor acceleration of development would appear to occur.

Eggs of *Mamestra configurata* react similarly to those of the saltmarsh caterpillar, *Estigmene acrea*, when exposed to 35.0 C (Fry and Surber, 1971). This suggests that eggs of *Mamestra configurata* are sufficiently tolerant to survive temperatures found in the south-western United States if the ovipositional period of *Mamestra configurata* there is similar to that of *Estigmene acrea*.

Effects of daily alternation between temperatures of 5.0 C and 20.0 C on eggs of different ages. – The effects of daily exposure to 5.0 C are more applicable to conditions found in Alberta. This experiment showed that eggs of *Mamestra configurata* are well adjusted to Alberta climatic conditions. Temperatures of 5.0 C, when alternated with a favourable temperature (20.0 C), do not have an appreciable effect on mortality (Tables 18–21). The only instance of high mortality was when eggs were exposed to 5.0 C for more than 22 hours daily. In these, hatching occurred only in the 96 hour group (Table 21) even though development to the black head capsule stage occurred in all eggs tested. Failure of these eggs to hatch was probably because the larvae within were debilitated by long exposure to 5.0 C. These results compare favourably with those of Lin *et al.* (1954) who found that as little as one hour per day spent at a favourable temperature allowed complete development of eggs of *Oncopeltus fasciatus*.

Time required for development was shorter under alternating than under constant temperature (Table 22). Similar results have been recorded for eggs of the noctuids *Agrotis orthogonia* and *Chorizagrotis auxiliaris* (Cook, 1927). There are two reasons for this apparent acceleration: (1) some development is taking place at 5.0 C (see Ms p 13), and (2) due to the sigmoidal nature of the temperature-rate of development curve, lower temperatures (5.0 C) contribute less to total development

than do those above the mean (Johnson, 1940).

Evolutionary and practical considerations

It is probable that the species *Mamestra configurata* originated further south and has gradually expanded its range northward. This would explain the existence of the partial second generation which still occurs in Alberta. Eggs of *Mamestra configurata* also show some resistance to temperatures that they are unlikely to experience in Alberta.

Results of this study, hopefully, will be used to remove some of the guesswork in making larval surveys of this insect. Even working with only mean, minimum and maximum temperatures, it will be possible to estimate hatching with some accuracy. Proper timing of the survey will allow for implementation of a more efficient control program. Up until now, control was not usually begun until the larvae had reached at least the fourth instar and caused considerable damage. Control measures directed against earlier instars will result in less damage occurring and in better control.

Further investigation should be conducted to determine if 30.0 C is actually the upper development-hatching threshold. Larvae which survived either constant high or low temperatures during embryogenesis should be reared to adulthood to determine what, if any, effects these treatments have on larvae, pupae, and adults.

The effects of humidity should be studied in greater detail to find out the mechanism or mechanisms by which development is affected. A possible starting point would be to determine if eggs of *Mamestra configurata* absorb moisture and if so to find out whether it is an active or a passive process. Additional field research is necessary to determine the relationships existing between air temperature, relative humidity, and micro-climate in rape fields and the effects of these on embryonic and larval development in *Mamestra configurata*. Predictions based only on general air temperature and relative humidity data may not be as reliable (Bursell, 1974).

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Guest Editorial – New Tools in Publishing

Although the acting editor of *Quaestiones Entomologicae* announced in his editorial “To compute or not compute” (*Quaestiones Entomologicae* Vol. 15(1): 119) that *Quaestiones Entomologicae* is now produced by the computer, you may not be aware that techniques used to produce this journal are among the more innovative in the publishing industry. Since *Quaestiones Entomologicae* was the first periodical at The University of Alberta to change to the new system, I would like to give an explanation of what is involved.

The traditional approach to publishing is fairly costly, due to the number of times a document must be typed. A manuscript, for example, may be typed several times before the author is satisfied. Reviewers may suggest further changes; and then it must be typed again for submission to a journal.

Once the manuscript is received by the publisher, the cycle starts over again. Although *Quaestiones Entomologicae* had previously been prepared by a typewriter which produced high quality copy, it was not much ‘smarter’ than the average typewriter. The manuscript was typed, page numbers applied, and then it was returned to the author to be proofread. At this point, further changes or corrections had to be cut and pasted onto the pages. Resulting changes to page make-up often entailed extensive revisions.

Clearly, the possibility for error increased each time a document was reworked. This meant that proofreading was necessary at each stage, making the entire job quite tedious.

The decision to turn to the computer is often prompted by the rumor that ‘the computer does it automatically’. Anyone who is apprehensive about this statement should be — the amount of time and effort required to make a system ‘automatic’ can be considerable. However, the ultimate benefit lies in the computer’s power to eliminate repetitive tasks. For a manuscript, entire pages need not be retyped to accommodate extra words or editorial changes and repositioning of each page is under program control.

A text formatting program reads material that has been entered into the computer from terminals or magnetic tape. Instructions are inserted in the text to tell the program when to begin new paragraphs, italicize text, or store words for the index. The program decides how much text will fit on a line, and begins a new page automatically whenever the current one is full. Page numbers and running titles also appear without prompting. As the program prepares the pages, it collects entries for the index, along with current page number. When the entire manuscript has been processed by the program, index entries are sorted alphabetically and printed.

If text is subsequently altered or edited, lines or paragraphs may fall on a different page. The program repositions the text, and makes necessary changes in the index. This means that once text is in the computer, it never needs to be entirely retyped. Corrections or additions are made where necessary; the program makes necessary adjustments to the format of pages.

In a journal such as *Quaestiones Entomologicae*, one of the greatest benefits is the automatic indexing. At the end of the year, when the entire volume has been entered into the computer, the index will be complete. The program will process all the manuscripts as one, and compile a comprehensive index.

Quaestiones Entomologicae is prepared using the TEXTFORM® program, which was implemented by a group in the Department of Computing Services at the University of Alberta. In 1975, when plans for TEXTFORM began, several text formatting programs were already available. Most, however, seemed inflexible, or were tailored specifically for typesetting. TEXTFORM was designed to format documents on a variety of devices, without changes to the instructions used in the text. Documents ranging from short reports to large scholarly texts are now produced on computer printers, plotting devices, and phototypesetters. The computing and typesetting experience of the users varies from novice to sophisticated.

As an author, you may feel that the new procedures will have little effect on you. However, you can be of assistance if you are near a computing centre and are able to supply to *Quaestiones Entomologicae* your manuscript in machine-readable form on a magnetic tape, rather than typed in the conventional manner. As long as the tape is 9-track, containing alphanumeric data coded in EBCDIC or ASCII, or a 7-track tape coded in BCD, it can be read at this computing centre. Be sure to indicate "DO NOT X-RAY" on the outside of the package, if you send a magnetic tape through the mail.

Further developments may also affect the traditional publishing process. Technology is now available to allow computers in Canada, the United States, and eventually other countries throughout the world, to communicate via telephone lines. If you are near a computing centre which is taking part in these developments, you may be able to access the computer at this university to check the final copy of your manuscript, rather than waiting for it to be sent through the mail.

Procedures in the publishing industry have been relatively constant in the past several hundred years. Changes are now taking place which will have a dramatic effect on information sharing. From seemingly remote locations, we may be able to browse through publications housed in other centres.

When the decision was made, converting to the computer may have been a drastic step for *Quaestiones Entomologicae*. However, if present publishing trends continue (as they undoubtedly will) the recent change at *Quaestiones Entomologicae* will not be the last.

Debra Reinhart
Publications Consultant
Department of Printing Services
University of Alberta
Edmonton, Alberta, Canada

COMPARATIVE STRUCTURE OF COMPOUND EYES OF CICINDELIDAE AND CARABIDAE (COLEOPTERA): EVOLUTION OF SCOTOPY AND PHOTOPY

J.E. KUSTER¹

Department of Entomology

University of Alberta

Edmonton, Alberta, Canada

T6G 2E3

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Compound eyes of males of Amblycheila schwarzi Horn, Omus californicus californicus Horn, Megacephala carolina mexicana Gray, and Cicindela tranquebarica Herbst, North American Cicindelidae, were examined by light and scanning electron microscopy. Intergeneric statistical analyses were made using data from visual field areas and from measurements of eye structures. Comparisons based on eye size showed two groups: small eyes, nocturnal A. schwarzi and nocturnal O. californicus; and large eyes, crepuscular M. carolina and diurnal C. tranquebarica adults. Three categories for probable eye function were shown: scotopic A, A. schwarzi and M. carolina; scotopic B, O. californicus; and photopic, C. tranquebarica adults. Photopic eyes also occur in these other cicindelids examined: Cicindela belfragei Sallé, Cicindela limbata nympha Casey, Cicindela limbalis Klug, Cicindela repanda repanda Dejean, and Cicindela longilabris Say. However, eyes of crepuscular adults of Cicindela lepida Dejean are scotopic A, although these beetles are in the large eye group. The plesiotypic character state of eye structure and function in cicindelid adults is scotopic A; the apotypic state is photopic. C. lepida adults have secondarily evolved scotopic A eyes.

Cicindelid eye structure and probable function was compared with that of two representatives of their sister family, the Carabidae. Adult nocturnal Pterostichus melanarius Illiger are small-eyed and in the scotopic B functional category; diurnal Elaphrus americanus Dejean are large-eyed and photopic. It is concluded that scotopy and photopy have evolved through parallelism in these sister taxa.

All beetle eyes examined are eucone and have a "subcorneal layer" between corneal lenses and crystalline cones. They have a distal rhabdomere composed of microvilli from only retinula cell seven, a more proximal, rectangular fused rhabdom formed from six retinula cells, and a basal eighth retinula cell with a rhabdomere. Large bulbous eyes of diurnal and crepuscular beetles have interfacetal mechanoreceptors.

Les yeux composées des mâles de quatre espèces nord-américaines de Cicindelidae, Amblycheila schwarzi W. Horn, Omus californicus californicus W. Horn, Megacephala carolina mexicana Gray et Cicindela tranquebarica Herbst, sont étudiés au microscope optique et au microscope à balayage électronique. Les aires de champ visuel ainsi que différentes mesures structurales des yeux sont comparées statistiquement entre les genres. L'analyse de la grosseur des yeux révèle deux groupes; petits yeux chez les espèces nocturnes A. schwarzi et O. californicus, et grands yeux chez l'espèce crépusculaire M. carolina et chez l'espèce diurne C. tranquebarica. Trois catégories sont mises en évidence quant à la fonction probable des yeux: yeux scotopiques A chez A. schwarzi et M. carolina, yeux scotopiques B chez O. californicus, et yeux photopiques chez C. tranquebarica. C. belfragei, Sallé, C. limbalis Klug, C. repanda repanda Dejean, C. longilabris Say et C. limbata nympha Casey ont aussi des yeux photopiques. Cependant les adultes de l'espèce crépusculaire C. lepida Dejean ont des yeux scotopiques A, bien qu'ils se classent parmi le groupe à grands yeux. La structure et la fonction scotopique A consistent la condition plésiotypique des yeux des Cicindelidae adultes, alors que le type photopique est la condition apotypique. Le type scotopique A que possèdent les adultes de C. lepida a évolué secondairement.

¹Present address: Department of Biology, York University, Downsview, Ontario, M3J 1P3

La structure et la fonction probable des yeux Cicindelidae ont été comparées à ceux de deux représentants des Carabidae, leur famille apparentée. Les adultes de l'espèce nocturne Pterostichus melanarius Illiger ont de petits yeux du type scotopique R; l'espèce diurne Elaphrus americanus Dejean a de grands yeux photopiques. Il est conclu que la vision scotopique et la vision photopique ont évolué parallèlement chez ces taxons apparentés.

Tous les yeux de Coléoptères examinés sont eucones et ont une "couche subcornéenne" entre les lentilles cornéennes et les cônes cristallins. Ils ont un rhabdomère distal, composé de microvillosités à partir de la septième cellule rétinienne seulement, un rhabdome plus proximal, rectangulaire et fusionné, formé de six cellules rétiennes, et un huitième cellule rétinienne basale, possédant un rhabdomère. Les grands yeux globuleux des espèces diurnes et crépusculaires ont des mécanorécepteurs entre leurs facettes.

INTRODUCTION

On the basis of ecological correlations, Exner (1891) classified insect compound eyes into two structural and functional categories. Apposition eyes are characteristic of diurnal insects active in bright sunlight and superposition eyes are adapted for vision of crepuscular and nocturnal insects. Recently functional categories for compound eyes have been borrowed from terms used for cone and rod visual systems of vertebrate retina, (Goldsmith and Bernard, 1974), respectively, *photopic* and *scotopic*. In scotopic eyes, a transparent zone or "crystalline tract" is formed either as an extension of Semper cells (Horridge, 1968, 1969), or by the distal non-rhabdomeric portions of the retinula cells (Miller *et al.*, 1968; and Døving and Miller, 1969). Horridge (1971) showed that in clear zone scotopic eyes, light entering many lenses is scattered upon several rhabdoms thus increasing light intensity, but decreasing image resolution of individual ommatidia (Horridge *et al.*, 1972; and Horridge, 1975). In photopic eyes such scattering of light does not occur (Varela and Wiitanen, 1970) and less than one percent of the light captured by a rhabdom is received through neighbouring lenses (Shaw, 1969).

Eyes of males of one species of each of the four North American genera of *Cicindela* (Coleoptera) have been examined: *Amblycheila schwarzi* Horn; *Omus californicus californicus* Horn; *Megacephala carolina mexicana* Gray; and *Cicindela tranquebarica* Herbst. Since adults of *Cicindela lepida* Dejean and *Cicindela belfragei* Sallé have apparently become secondarily crepuscular, their eye structures are also described to determine if these eyes have evolved in response to this diel behavioural adaptation.

The question arises as to why tiger beetles were chosen for a detailed examination of eye structure and function from an evolutionary approach? This bias is based on my hypothesis, that since there is a behavioural transformation series from a plesiotypic (ancestral) nocturnal through crepuscular to the apotypic (derived) diurnal diel activity within the four North American genera of cicindelids, that there may also be a parallel transformation series in structure and function of their compound eyes. I therefore believe this to be evolution of eye structure and function in relation to diel activity.

The only detailed research on larval stemmata and adult compound eye structure and function of some species of *Cicindela* is that by Friedrichs (1931). On questioning the structural attributes of eyes of individuals of other cicindelid genera, he wrote (translated from the German): "It would be particularly interesting to establish in what manner the eyes of these nocturnal and crepuscular cicindelids have been adapted to their way of life: It may well be assumed that superposition [scotopic] eyes with pigment displacement have been formed, while the day-running or flying cicindelids possess apposition [photopic] eyes (like *Cicindela*)."

To answer some of Friedrichs' questions, this paper provides descriptions of eye structures based on histological examination; descriptions of the relationships of eye size groups, eye function categories, and diel activities in terms of a reconstructed phylogeny of the Cicindelidae.

Structure and function of cicindelid eyes are then compared to eyes of individuals of their sister family, the Carabidae, to determine if carabids with similar diel activity have evolved similar eye structures. To answer this question, eyes of adults of nocturnal *Pterostichus melanarius* Illiger, and

diurnal *Elaphrus americanus* Dejean are described. Eye structure is then related to eye size groups and eye function categories of the cicindelids and the phylogeny of these sister taxa.

MATERIALS AND METHODS

For scanning electron microscopy (SEM), beetle heads were washed in Tide[®] laundry detergent, rinsed in distilled water, then fixed in 5% formalin. After ethanolic dehydration, heads were cleared in xylol and air-dried overnight (Hollenberg and Erickson, 1973). The heads were carbon and gold coated to a thickness of 15–20 nm using an Edwards 12E vacuum evaporator, then examined with a Cambridge Stereoscan S4 Scanning Electron Microscope at accelerating voltages of 20–30 kV. Histological material for light microscopy (LM) was fixed in hot 80% ethanolic Bouin's Duboscq (Pantin, 1962). Dark-adapted beetles were deprived of light for five days prior to fixation. Excised eyes were dehydrated in tertiary butanol then double-embedded using Peterfi's celloidin-paraffin technique (Pantin, 1962). To facilitate sectioning of these hard beetle heads, the knife and wax blocks were chilled. Sections were cut at 10–12 μ m using a Leitz Wetzlar microtome. Longitudinal and transverse sections were treated in a saturated mercuric chloride containing 5% acetic acid mordant solution (Pantin, 1962). Precipitations of mercurous chloride and metallic mercury were removed using Gram's variation of Lugol's iodine solution. A 5% sodium thiosulfate solution removed Lugol's solution (Humason, 1962). Sections were stained with Mallory's triple stain (Pantin, 1962) and mounted with Canada balsam. Representative photographs were taken using a Carl Zeitz Ultraphot II.

Measurements of structures for ratios were randomly chosen and calculated as $\bar{x} \pm \text{SE}$ for a sample size of five. The retinulae were assumed to be a cylinder consisting of three portions: the clear zone, rhabdom zone, and basal zone. These volumes and the volumes of the rhabdom zone of the basal retinula cell were calculated as cylinders. Volumes of the rhabdom of the retinula rhabdom zones were calculated as a solid rectangle. Comparative measurement data were statistically analyzed using computer programs for One-Way Analysis of Variance and Duncan's New Multiple Range Test of Means (Sokal and Rohlf, 1969). Using the statistical groupings resulting from Duncan's test, measurements were either tabulated in the eye size or eye functional category.

RESULTS

Structure of eyes of one species of each of the four North American genera of cicindelid adults

Eyes of the nocturnal genera, *Amblycheila schwarzi* (Fig. 1) and *Omus californicus* (Fig. 2) have small, relatively flat eyes compared with the large bulbous eyes of crepuscular *Megacephala carolina* (Fig. 3) and diurnal *Cicindela tranquebarica* adults (Fig. 4). The vertexes (v) of the latter two beetle heads are concave, allowing the eyes to extend above the top of the heads. Figures 5–8 (Kuster, 1975) show that representative compound eyes of all four genera are convex and outer surfaces consist of convex, hexagonal corneal lenses (l). A ring of cuticle, the ocular sclerite (os), defines the border of the eyes. Because of eye size and shape differences, each beetle has a variable anterior, posterior, and dorsal stereoscopic area of the visual field (Kuster, 1978).

Table 1 shows that adults of nocturnal cicindelids have fewer ommatidia than have adults of diurnal-crepuscular beetles. In representatives of nocturnal genera, eyes span less than one-third the head width, but in crepuscular and diurnal genera, eyes occupy approximately one-half of the head width. From values comparing eye height to head height, neither eyes of *Amblycheila schwarzi* or *Omus californicus* adults extend above the vertex as do those of *Megacephala carolina* and *Cicindela tranquebarica*. It is possible therefore to assume that both *Cicindela tranquebarica* and *Megacephala*

carolina adults see above the head, but that vision above the vertex is less for eyes of *Amblycheila schwarzi* and *Omus californicus* adults. Ratios of head width to pronotum width indicate that neither adults of *Amblycheila schwarzi* nor *Omus californicus* can see behind their pronota. However, both representatives of *Megacephala carolina* and *Cicindela tranquebarica* have this ability. None of these adult tiger beetles can see behind their elytral margins. However, the list of ratios (Table 1) does not indicate the absolute limits of vision. Tiger beetles display an alert behavioural stance by rearing up on the prothoracic legs so that the abdomen is pressed to the substrate (Swiecinski, 1957; Willis, 1967). Such a stance may permit the beetles to see more of their environment in the anterior and posterior directions.

Ommatidia of insect compound eyes can be divided into two distinct structural and functional regions: the light receiving or dioptric apparatus, with its associated primary pigment cells and the retinula with its associated secondary and basal pigment cells.

Figures 9–12 are representative longitudinal, and figures 13–16, representative transverse sections, through compound eyes of one species from each of the four cicindelid genera. These figures show lamellated corneal lenses (l) having distal acidophilic thin corneal layer (t), and crystalline cones (c) with four quadrants. Normally, the dioptric apparatus of eucone eyes (*sensu* Grenacher, 1879) consists solely of these two structures. However, in cicindelid beetle eyes, an acidophilic, lamellated third layer has been discovered between the lens and the cone. This layer is termed the “subcorneal layer” (cl) because of its position and structural similarity to the corneal lens. These beetle eyes therefore, have a three layered dioptric apparatus. Figures 17–20 show that corneal lenses (l) are apparently convex distally and hexagonal in shape. None of the lenses have corneal nipples (Bernhard *et al.*, 1965). Scattered between lenses of adult eyes of *Megacephala carolina* (Fig. 19) and *Cicindela tranquebarica* (Fig. 20) are conical interfacetal cuticular pegs (cp). There is approximately one peg per 20 ommatidia with a total of approximately 210 per eye in adults of *Megacephala carolina* and one peg per 15 ommatidia (total 260) on eyes of *Cicindela tranquebarica* adults. Pegs are slightly taller and wider in eyes of *Cicindela tranquebarica* (Table 1).

Although not resolvable in figures 9–16, two primary pigment cells which are devoid of pigment granules, surround the crystalline cones. Oblique light rays entering the eyes, which cannot be refracted by the dioptric apparatus, are absorbed laterally by pigment granules in secondary pigment cells (2p). Secondary pigment granules are more densely aggregated and appear black in eyes of nocturnal *Amblycheila schwarzi* (Fig. 9,13) and *Omus californicus* adults (Fig. 10,14), compared to the less dense brown pigment granules in eyes of *Megacephala carolina* (Fig. 11,15) and *Cicindela tranquebarica* (Fig. 12,16).

The dioptric apparatus is connected to the retinula by a crystalline thread which is shrouded by secondary pigment cells. This thread is an extension from each of the four Semper cells which surround the crystalline cone quadrants.

The retinula extends proximally from the proximal tip of the crystalline thread to the basement membrane (bm). A cluster of seven neurons of retinula cells constitute an ommatidial retinula. In all cicindelid beetle eyes examined, microvilli from retinula cell seven form a distal rhabdomere. Retinula cells of *Amblycheila schwarzi* (Fig. 9,13) and of *Megacephala carolina* adults (Fig. 11,15) consist of a clear retinula zone (cr) and a proximal retinula rhabdom zone (rr). Retinula of eyes of *Omus californicus* (Fig. 10,14) and of *Cicindela tranquebarica* (Fig. 12,16) have no clear retinula zone. All have a basal retinula zone (br) of an eighth retinula cell with a rhabdomere.

The rhabdom zone consists of a rectangular, fused rhabdom (r) in the centre of six retinula cells (rt) (Fig. 21–24). Two retinula cells contribute microvilli to form the rhabdom of the wide sides; one cell contributes to each short side. The rhabdom occupies a greater percentage of retinula cell surface area

and volume (Table 3) in eyes of *Amblycheila schwarzi* (Fig. 21) and *Megacephala carolina* (Fig. 23) than in *Omus californicus* (Fig. 22) or *Cicindela tranquebarica* adults (Fig. 24). The retinula cytoplasm in eyes of *Cicindela tranquebarica* adults is distinctly visible. In all four beetle eyes, the vacuolated seventh retinula cell is positioned lateral to the rhabdom and does not contribute a rhabdomere at this level. Sixteen secondary pigment cells (2p) surround the retinula and four basal pigment cells (bp) surround the basal retinula cell.

Each of the eight retinula cells extends an axon (a) to interneurons in the lamina ganglionaris (lg) (Fig. 9–12). Eight axons from each ommatidium penetrate a single circular fenestration in the tracheole-rich basement membrane, and are aggregated with axons of five adjacent ommatidia in the form of axonal bundles distal to the lamina ganglionaris. Evident from figures 25–28, axonal bundles (ab) of eyes of *Amblycheila schwarzi* adults are much longer than those in other beetle eyes. Glial cells (gl) surround axons. The probable neuronal pathway through the brain is suggested in these figures. Following synapsis lamina interneurons, axons cross over at the first optic chiasmata (1c), then extend to the medulla (md), the second synaptic site of the optic lobe. Visual axons again cross over at the second optic chiasmata (2c), followed by proximal synapsis in the third region of the optic lobe, the lobula (lo). Optic lobes consist of a connective tissue sheath, the neurilemma (nl), an underlying cellular perineurium (pn) with glial and neuronal cell bodies, and a central neuropile of axons and dendrites. A large pigment accumulation (pa) is on the ventral aspect of the interface of the lamina and medulla of the optic lobe (see also Fig. 12).

After dark adaptation for five days, structures of the eyes of *Cicindela tranquebarica* adults were examined. Only minor changes occurred when compared to light-adapted eyes. In eyes of these beetles, pigment granules in secondary pigment cells migrated distally around crystalline cones and proximally around basal retinula cells leaving little pigmentation surrounding retinulae. This is assuming that the same pattern of orientation of pigments is not altered by fixation and dehydration. Shortening of the crystalline threads to approximately half their length in the light-adapted state was the most striking change.

Structures of representative ommatidia are summarized diagrammatically in figures 29–32. Table 1 and 3 provide measurements from five ommatidia chosen randomly.

Structure of eyes of *Cicindela lepida* and *Cicindela belfragei* adults

Figure 33, of the head of an *Cicindela lepida* adult shows large bulbous eyes, similar in shape (Fig. 34) to those of *Cicindela tranquebarica* adults (Fig. 4). Corneal lenses (l) (Fig. 35) and interfacetal pegs (cp) (Fig. 36) are typical of *Cicindela* adults. The corneal layer (t) is relatively thin. From longitudinal (Fig. 37) and transverse sections (Fig. 38) of the eye, the cellular organization is similar to that of eyes of *Megacephala carolina* adults (Fig. 11,15). A clear retinula zone (cr) is present. The surface area of the rhabdom (r) (Fig. 39) is moderately large.

Light-adapted eyes of *Cicindela lepida* adults show lengthening of crystalline threads, shortening, but not disappearance of the clear retinula zone. A more even distribution of pigment granules in secondary pigment cells also occurs along the length of retinulae compared to dark-adapted *Cicindela lepida* eyes collected at twilight.

Eye shape (Fig. 40,41), corneal lenses (l) (Fig. 42) and cuticular pegs (cp) (Fig. 43) of eyes of *Cicindela belfragei* adults are similar to those of other *Cicindela* adults. Cellular organization for vision (Fig. 44,45) is similar to that of *Cicindela tranquebarica* eyes (Fig. 12,16). There is no clear retinula zone. The surface area of the rhabdom (r) (Fig. 46) is small.

Structure of eyes of *Pterostichus melanarius* and *Elaphrus americanus* carabid adults

The head of *Pterostichus melanarius* adult (Fig. 47) has a convex vertex like that of *Amblycheila schwarzi* and of *Omus californicus* adults (Fig. 1,2). Eyes are small and spherical (Fig. 48) as are those of *Amblycheila schwarzi* adults (Fig. 5). Hexagonal, convex corneal lenses (l) (Fig. 49) have a thin corneal layer, but no interfacetal pegs. Material (x) secreted from dermal glands (Fig. 50) may be used as grooming lubricant to clean the eye, or may contribute to the composition of the thin corneal layer. These eyes have no clear retinula zone (Fig. 51,52) like eyes of *Omus californicus* adults (Fig. 10,14), but the rhabdom (r) has a large cross-sectional surface area (Fig. 53) compared to that of the rhabdom of *Amblycheila schwarzi* eyes (Fig. 24).

Vertices of *Elaphrus americanus* adults are convex, however, their eyes are bulbous and extend above the vertex (Fig. 54). They are similar in shape (Fig. 55) to eyes of *Megacephala carolina* adults (Fig. 7), and those of other *Cicindela* adults (Fig. 8,34,41). Hexagonal corneal lenses (l) are well defined (Fig. 56) due to their degree of convexity, and are similar to those of *Cicindela* adults (Fig. 20,35,42). Interfacetal pegs (cp) (Fig. 57) are present. There is no clear retinula zone (Fig. 58,59) and these eyes have a similar cellular organization to eyes of *Cicindela tranquebarica* (Fig. 12,16) and *Cicindela belfragei* (Fig. 44,45). The rhabdom (r) (Fig. 60) has a small surface area.

Eye size groups and functional categories of cicindelid beetle eyes based on measurements of structures

From statistical inference using One-Way Analysis of Variance and Duncan's Range Test of Means, measurement data were grouped either into eye size or eye function categories.

Eye size groups. – When structural measurements are related to eye size, adults of the four North American genera of Cicindelidae can be divided into two groups (Table 1): Small Eye Group: eyes of adults of *Amblycheila schwarzi*; *Omus californicus*. Large Eye Group: adults of *Megacephala carolina*; *Cicindela tranquebarica*; *Cicindela lepida* and *Cicindela belfragei*.

For clarification of small eye size relationships of cicindelid taxa, the similarity matrix (Table 2) is included. The data for Table 2 are summations of statistically similar structures at $P = 0.01\%$ from Table 1. Based on these totals, there are trends in similarities within eye size groups and differences between these two groups among the cicindelids. Note that of 39 characters, small eyes of nocturnal *Amblycheila schwarzi* and *Omus californicus* share 21 characters; large eyes of crepuscular *Megacephala carolina* and diurnal *Cicindela tranquebarica* adults share 16 characters. Also eyes of the adults of *Cicindela* spp. share several attributes.

Unlike the diurnal and crepuscular beetles, nocturnal cicindelids possess small eyes with fewer ommatida and no interfacetal pegs. Smaller visual fields are characteristic of eyes of these beetles, as demonstrated by head, thorax, and elytral ratios, and from forward and dorsal Mollweide homolographic projections. (Kuster, 1978). Corneal lenses are long in these eyes, while crystalline cones of diurnal-crepuscular large eyes occupy a larger percentage of dioptric apparatus lengths. The dioptric apparatus occupies over half the ommatidial length in small-eyed beetles; but only approximately one-third the ommatidial length in the large eye group. Characteristic of large cicindelid eyes are crystalline threads almost twice as long as in the small eye group. Retinulae extend only slightly over one-third the ommatidial length of the small eye group but over half this length in the large eye group. Retinulae extend only slightly over one-third the ommatidial length of the small eye group but over half this length in the large eye group. Basal retinula zones are longer in the small eye group. There is also a similarity in nocturnal beetles concerning rhabdom zone volume and retinula and rhabdomeric volumes of ommatida and compound eyes, all of which are smaller than volumes of the long retinula and rhabdoms of large eyes.

Table 1. Arrangement of six cicindelid beetles into two groups based on eye size. The values are \bar{x} for $n = 5$ for each species. Solid underscore represents no statistically significant difference at $P = 0.05\%$. Dashed underscore represents no statistically significant difference at $P = 0.01\%$. Absence of an underscore indicates statistically difference. 0 indicates no such structure exists for that species and — indicates no measurement made.

Measurements	<i>Amblycheila schwarzi</i>	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Cicindela lepida</i>	<i>Cicindela belfragei</i>
Eye size group	Small	Small	Large	Large	Large	Large
Diel activity	Nocturnal	Nocturnal	Crepuscular	Diurnal	Crepuscular	Crepuscular
Number of ommatidia	1,700	1,500	4,200	4,000	3,200	3,800
<u>Number of ommatidia</u>						
Antennal length	89.60	167.17	323.79	498.53	—	—
<u>Eye width</u>						
Head width	23.70	26.88	41.50	55.10	—	—
<u>Eye height</u>						
Head height	91.18	92.58	105.54	112.60	—	—
<u>Head width</u>	84.30	85.80	104.70	108.48	—	—
Pronotum width						
<u>Head width</u>	66.90	66.10	76.20	63.90	—	—
Elytra width						
Mollweide projection of % forward visual field areas ($n = 3$)						
Monoscopic	89.65	86.87	71.76	60.62	—	—
Stereoscopic frons	4.30	10.26	15.19	23.21	—	—
Stereoscopic behind	4.53	2.63	13.05	16.07	—	—
Total stereoscopic	8.83	12.89	28.24	39.38		
Blind frons	0.48	0	0	0	—	—
Blind behind	1.04	0.24	0	0	—	—
Total blind	1.52	0.24	0	0	—	—
Diameter of crystalline cone	18.60	17.44	16.28	16.28	16.08	15.46
Total length of dioptric apparatus	176.65	145.56	136.48	126.05	99.19	101.24
Length of crystalline thread	23.25	13.95	60.45	51.15	7.08	9.08
Length of retinula						
(a) Rhabdom zone	58.13	86.03	102.30	186.00	90.00	121.50
(b) Basal zone	20.93	16.28	18.60	18.60	18.00	13.50
Total length of retinula	123.24	102.31	232.50	204.60	184.50	135.00
Total length of ommatidia	323.14	261.82	429.43	381.80	290.77	245.32
Dimensions of rhabdom						
(a) Diameter of basal zone	4.65	4.65	6.95	5.79	4.54	2.72
Length of dioptric apparatus						
Length of ommatidium	54.67	55.59	31.78	33.01	34.12	41.27
Length of crystalline thread						
Length of ommatidium	7.20	5.33	14.08	13.40	2.43	3.70
Length of retinula						
Length of ommatidium	38.13	39.08	54.14	53.59	63.45	55.03
Volume of retinula (μm^3)						
(a) Rhabdom zone	7468.46	9129.01	13143.37	24498.66	9105.93	7867.62

Table 1. (continued)

Measurements	<i>Amblycheila schwarzi</i>	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Cicindela lepida</i>	<i>Cicindela belfragei</i>
Volume of retinula Ommatidium	11411.25	11627.25	18686.05	26474.55	13239.55	8359.24
Volume of retinula Compound eye	19.40(10 ⁶)	17.44(10 ⁶)	78.48(10 ⁶)	105.90(10 ⁶)	42.37(10 ⁶)	31.77(10 ⁶)
Volume of rhabdom Compound eye	8.09(10 ⁶)	5.65(10 ⁶)	43.64(10 ⁶)	16.84(10 ⁶)	18.74(10 ⁶)	5.67(10 ⁶)
Length of corneal lens (μm)	111.60	106.95	74.40	67.43	47.67	56.75
Height of interfacetal peg	0	0	3.08	3.12	2.45	2.54
Diameter of interfacetal peg	0	0	2.28	2.32	1.91	2.00
Length of crystalline cone	60.45	334.58	55.80	53.48	47.67	40.86
Mollweide projection of % dorsal visual field areas (n = 3)						
Monoscopic	89.65	86.87	71.76	60.62	—	—
Stereoscopic vertex	8.19	7.24	20.68	24.90	—	—
Stereoscopic mouth to neck	0.64	5.65	7.56	14.48	—	—
Total stereoscopic	8.83	12.89	28.24	39.38	—	—
Blind vertex	0.33	0.16	0	0	—	—
Blind mouth to neck	1.19	0.08	0	0	—	—
Total Blind	1.59	0.24	0	0	—	—

Table 2. Similarity matrix for six cicindelid beetles based on eye size groups. For *Amblycheila schwarzi*, *Omus californicus*, *Megacephala carolina*, *Cicindela tranquebarica* there are 39 characters. When all six beetles are compared there are 20 characters in common available.

Tiger Beetle	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Cicindela lepida</i>	<i>Cicindela belfragei</i>
<i>Amblycheila schwarzi</i>	21	3	3	2	3
<i>Omus californicus</i>		6	4	6	7
<i>Megacephala carolina</i>			16	4	5
<i>Cicindela tranquebarica</i>				8	5
<i>Cicindela lepida</i>					11

Eye functional categories. – When structures involved with function of cicindelid compound eyes are statistically analyzed, three functional categories can be inferred (Table 3): Scotopic A: eyes of representative adults of *Amblycheila schwarzi*; *Megacephala carolina* and *Cicindela lepida*. Scotopic B: eyes of adults of *Omus californicus*. Photopic: eyes of adults of *Cicindela tranquebarica*, and *Cicindela belfragei*.

For clarification of functional eye categories of cicindelid taxa, the similarity matrix (Table 4) is included. The data for Table 4 are summations of statistically similar structures at $P = 0.01\%$ from Table 3. Based on these totals, there are trends in similarities within categories of eye function and differences among these three categories within the cicindelids.

Beetles included in the scotopic A functional category have relatively long antennae which may permit increased touch and olfactory stimulation in addition to sight. The thin corneal layers of these eyes are relatively thick, but the subcorneal layers are relatively thin. Eyes of adult *Amblycheila schwarzi*, *Megacephala carolina* and *Cicindela limbalis* have clear retinula zones and although less than half these retinula lengths are rhabdomeric, these rhabdoms have very large surface areas. Volume of rhabdom zones are greater in eyes of *Amblycheila schwarzi* than those of *Omus californicus*, its small-eyed counterpart. It is larger in eyes of *Megacephala carolina* than its large-eyed counterparts, *Cicindela tranquebarica*, *Cicindela limbalis* and *Cicindela belfragei*. Percentage rhabdom zone volume of retinulae are smaller in scotopic A eyes due to the presence of clear retinula zones. However, total volume of the rhabdom per ommatidium is larger in scotopic A eyes as is percentage of rhabdom volume to retinula volume since the rhabdom has such a large surface area.

Eyes of *Omus californicus* adults are scotopic B. Individuals of this species have short antennae and although their eyes possess many small-eyed structural similarities with those of *Amblycheila schwarzi* adults (Table 1), they can be grouped into a separate functional category. Like scotopic A eyes, these eyes have thin subcorneal layers, but thinner, thin corneal layers. Unlike the scotopic A eyes, there is no clear retinula zone. Although almost twice the retinula lengths are occupied by the rhabdom zone, surface areas and volumes of the rhabdom are smaller, as is percentage volume of the rhabdom to retinula volume in scotopic B and scotopic A eyes. Consequently, percentage volume of the retinula around the rhabdom and percentage volume of the rhabdom are larger in scotopic B ommatidia, but total retinula and rhabdom volumes are less in the whole scotopic B eye.

Cicindela tranquebarica and *Cicindela belfragei* adults have photopic eyes. Like adults of *Omus californicus*, these beetles have short antennae. But based on eye size, these eyes share structural similarities to eyes of *Megacephala carolina* adults since they are in the large eye group (Table 1). Photopic eyes of *Cicindela tranquebarica* and *Cicindela belfragei* adults have thick subcorneal layers, but like scotopic B eyes, have thin corneal layers, no clear retinula zone, and rhabdoms occupying almost the complete retinula length. Surface areas of rhabdoms are the smallest and rhabdom volumes are small considering retinulae lengths. Percentage rhabdom volume to retinula volume is very small but percentage of retinula volume surrounding the rhabdom is very large.

Eye size groups and functional categories of carabid beetle eyes based on measurements of structures

Eye size groups. – Cicindelid beetle eyes examined here can be placed into two groups based on eye size and into three functional categories. To test convergence of eye structure and function based on eye size, measurement of eyes of two carabid adults were statistically compared to those of four cicindelid sister taxa (for basic data, see Kuster, 1978).

According to eye size, cicindelid and carabid adults have similar eye structures (Table 5). Eyes of *Pterostichus melanarius* fit the small eye group; *Elaphrus americanus*, the large eye group. The data for Table 5 are summations of statistically similar structures at $P = 0.01\%$. Based on these totals, there are

Table 3. Arrangement of six cicindelid beetles into three categories based on eye function. The values are \bar{x} for $n = 5$ for each species. Solid underscore represents no statistically significance difference at $P = 0.05\%$. Dashed underscore represents no statistically significant difference at $P = 0.01\%$. Absence of an underscore indicates statistically difference. 0 indicates no such structure exists of that species and — indicates no measurement made.

Measurement	<i>Amblycheila schwarzi</i>	<i>Megacephala carolina</i>	<i>Cicindela lepida</i>	<i>Omus californicus</i>	<i>Cicindela belfragei</i>	<i>Cicindela tranquebarica</i>
Functional eye category	Scotopic A	Scotopic A	Scotopic A	Scotopic B	Photopic	Photopic
Eye size group	Small	Large	Large	Small	Large	Large
Diel activity	Nocturnal	Crepuscular	Crepuscular	Nocturnal	Crepuscular	Dirunal
Antennal length (mm)	18.98	12.98	—	8.98	—	8.00
Thickness of thin corneal layer (μm)	<u>2.27</u>	3.95	<u>1.58</u>	<u>1.70</u>	<u>1.36</u>	<u>1.65</u>
Diameter of corneal lens	<u>22.73</u>	<u>22.73</u>	<u>24.97</u>	<u>20.45</u>	<u>24.97</u>	<u>25.00</u>
Thickness of subcorneal layer	<u>2.33</u>	<u>2.33</u>	<u>2.27</u>	<u>2.33</u>	<u>2.27</u>	<u>3.49</u>
Volume of rhabdom						
(a) Rhabdom zone	<u>4400.56</u>	9684.56	<u>5564.70</u>	<u>3488.84</u>	1413.04	<u>3720.00</u>
(b) Basal zone	<u>355.44</u>	705.62	<u>291.39</u>	<u>276.47</u>	78.44	<u>489.72</u>
Surface area of rhabdom in rhabdom zone (μm^2)	75.70	94.67	61.83	40.55	<u>11.63</u>	<u>20.00</u>
Total volume of rhabdom Ommatidium	<u>4756.00</u>	10390.18	<u>5856.09</u>	<u>3765.31</u>	1491.48	<u>4209.73</u>
Rhabdom volume	41.68	55.60	44.23	32.38	<u>17.84</u>	<u>15.90</u>
Retinula volume						
Dimensions of rhabdom						
(a) Rhabdom zone						
Length	<u>9.30</u>	11.63	<u>9.08</u>	6.98	3.41	5.00
Width	<u>8.14</u>	<u>8.14</u>	6.81	5.81	<u>3.41</u>	<u>4.00</u>
Volume of retinula (μm^3)						
(a) Clear zone	743.84	<u>2699.85</u>	<u>2657.02</u>	0	0	0
(b) Basal zone	<u>3198.95</u>	<u>2842.83</u>	<u>1467.60</u>	<u>2488.24</u>	491.72	<u>1975.89</u>
Length of retinula						
(a) Clear zone	44.18	111.60	76.50	0	0	0
Dimensions of retinula						
(a) Diamter of clear zone	4.63	5.55	6.65	0	0	0
(b) Diameter of rhabdom zone	<u>12.79</u>	<u>12.79</u>	<u>11.53</u>	<u>11.63</u>	9.08	<u>12.95</u>
(c) Diameter of basal zone	<u>13.95</u>	<u>13.95</u>	10.22	<u>13.95</u>	6.81	11.63

trends in similarities within eye size groups and differences between these two groups between the cicindelids and carabids.

Although eyes of the carabids have fewer ommatidia, eyes of diurnal *Elaphrus americanus* adults have more ommatidia than eyes of nocturnal *Pterostichus melanarius*. Corneal lenses and crystalline cones are longer and no interfacetal pegs are present in the small of this nocturnal, carabid eyes. Lengths of crystalline threads of eyes of *Omus californicus* and *Elaphrus americanus* are similar, and crystalline threads of *Pterostichus melanarius*, and *Megacephala carolina* eyes are smaller in length. Basal retinula zone lengths and diameters are similar in all these beetle eyes except in those of *Elaphrus americanus* where they are half as large. Eyes of *Pterostichus melanarius* adults have longer retinulae similar to those of *Omus californicus* adults. Volume of the rhabdom zone of the retinula and retinula volume per eye are similar in *Omus californicus* and *Pterostichus melanarius* adults, and adults of *Elaphrus americanus*, *Amblycheila schwarzi* and *Omus californicus* since all these eyes have relatively short retinulae. Indicative of small eyes and nocturnal behaviour, both adults of *Amblycheila schwarzi* and *Pterostichus melanarius* have similar rhabdom volume per eye but the carabid has a rhabdom volume statistically similar to eyes of *Cicindela tranquebarica* adults because retinulae of this carabid are so short. Rhabdom volume of *Elaphrus americanus* adults is exceedingly small.

Eye functional categories. – Comparisons of functional aspects of the cellular organization for vision of cicindelid and carabid beetles show similarities (Table 6) (for basic data, see Kuster, 1978). Eyes of *Pterostichus melanarius* adults are grouped with eyes of *Omus californicus* adults in the scotopic B category; eyes of *Elaphrus americanus* adults in the photopic category with *Cicindela tranquebarica* adults. The data for Table 6 are summations of statistically similar structures at $P = 0.01\%$. Based on these totals, there are trends in similarities within the eye functional categories and differences among these three categories among the cicindelids and carabids.

Thickness of the thin corneal layer places eyes of *Pterostichus melanarius* close to those of *Amblycheila schwarzi* while the subcorneal layer of eyes of *Elaphrus americanus* adults, though thicker than that of *Pterostichus melanarius* is similar to that in eyes of adults of *Amblycheila schwarzi*, *Omus californicus* and *Megacephala carolina*. Diameters of retinulae of *Pterostichus melanarius* eyes are similar to those of *Omus californicus*, while basal zone diameters of the two carabid eyes are similar. Both lengths and widths of rhabdoms of *Pterostichus melanarius* eyes are similar to those of *Amblycheila schwarzi* adults, but the rhabdom of *Elaphrus americanus* like that of *Cicindela tranquebarica* adults, is exceedingly small with minimum surface area and volume.

DISCUSSION AND CONCLUSIONS

Dioptric apparatus

Adult eyes of representative species of North American genera of Cicindelidae and Carabidae have a eucone, three-layered dioptric apparatus. Although Gissler (1879) observed the corneal lens of adult *Omus* sp. and *Cicindela* sp. to be biconvex, and the cornea of adult *Amblycheila* sp. to be convex only interiorly, I have shown that adult eyes of species of these genera to have biconvex lenses. Confusion regarding corneal lens shape possibly resulted because the lenses of *Amblycheila schwarzi* and *Megacephala carolina* have relatively thick corneal layers which externally appear smooth. Thickness of this layer may be important in understanding difference in eye function. A thick layer may scatter incident light over many lenses so that light is shared by adjacent ommatidia. Because this corneal layer is thinner in eyes of *Omus californicus*, *Cicindela tranquebarica*, *Cicindela limbalis* and *Cicindela belfragei* adults, individual lenses are more distinctly separated and optical isolation is maintained between adjacent ommatidia, possible resulting in enhanced visual acuity. Scratches on this layer may result from burrowing or less likely from grooming activities.

Table 4. Similarity matrix for six cicindelid beetles based on eye function. For *Amblycheila schwarzi*, *Omus californicus*, *Megacephala carolina*, *Cicindela tranquebarica* there are 17 characters. When all six beetles are compared there are only 16 characters in common available.

Tiger Beetle	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Cicindela lepida</i>	<i>Cicindela belfragei</i>
<i>Amblycheila schwarzi</i>	8	6	5	6	2
<i>Omus californicus</i>		4	9	6	7
<i>Megacephala carolina</i>			4	3	2
<i>Cicindela tranquebarica</i>				4	8
<i>Cicindela lepida</i>					4

Table 5. Similarity matrix for four cicindelid and two carabid beetles based on eye size. There are 20 characters.

Beetle	<i>Amblycheila schwarzi</i>	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Pterostichus melanarius</i>
<i>Pterostichus melanarius</i>	8	8	4	4	20
<i>Elaphrus americanus</i>	5	6	2	1	5

Table 6. Similarity matrix for four cicindelid and two carabid beetles based on eye function. There are 16 characters.

Beetle	<i>Amblycheila schwarzi</i>	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Pterostichus melanarius</i>
<i>Pterostichus melanarius</i>	6	7	2	5	16
<i>Elaphrus americanus</i>	1	5	2	4	6

All cicindelid and carabid beetle eyes examined have a structurally distinct layer between the lens and cone termed the subcorneal layer. Eyes of adult *Notiophilus biguttatus* F. and *Loricera pilicornis* F. (Carabidae) also have this structure which Home (1976) terms the “proximal corneal layer”. From observations using Nomarski differential interference contrast microscopy, this layer is of intermediate refractive index between the lens and cone and therefore may function to bend incident light rays medially toward the crystalline cone (Kuster, 1978).

Interfacetal pegs

Both crepuscular and diurnal adult cicindelids and the diurnal carabid have interfacetal pegs between some corneal lenses. Nocturnal flightless cicindelids and the nocturnal carabid lack them. Since the pegs appear to lie on a cuticular articulating membrane and since there is no visible hole at the apex, it is assumed that these structures function as mechanoreceptors. Other adult beetles, capable of flight, such as *Creophilus erythrocephalus* F. and *Sartallus signatus* Sharp (Staphylinidae) also have interfacetal pegs (Meyer-Rochow, 1972) similar in size and shape to those described here. According to Nesse (1965, 1966) for *Apis mellifica* (= *Apis mellifera* Apidae) and Chi and Carlson (1976) for *Musca domestica* (Muscidae), and Honegger (1977) for *Gryllus campestris* L. (Gryllidae), these interfacetal mechanoreceptors sense the direction and relative velocity of passing over the eyes during flight and may play a role in eye cleaning behavior (Honegger)

Retinula cells and rhabdoms

It is important to emphasize that the difference in retinula and rhabdom structure of the cicindelid and carabid eyes investigated is not one of change in cell number, but is a difference in cellular organization which results in varied functional abilities of these eyes.

Scotopic A eyes

Retinulae of eyes of adults of *Amblycheila schwarzi*, *Megacephala carolina* and *Cicindela lepida* have a clear retinula zone or crystalline tract (*sensu* Døving and Miller, 1969) consisting of seven retinula cells which do not have a rhabdom at this level. Such a scotopic A retinula organization has also been observed in adult carabid beetle eyes such as those of *Carabus auratus* L. (Kirchoffer, 1905, 1908; Bernard, 1932; and Hasselmann, 1962), *Steropus madidus* Fab., and *Eutrichomerus terricola* Herbst (Bernard, 1932); and *Notonomus* sp. (Horridge and Giddings, 1971); and in the following dytiscids; *Dytiscus* sp. and *Cybister* sp. adults (Grenacher, 1879; Exner, 1891; Kirchoffer, 1908; Horridge, 1969; Horridge *et al.*, 1970; and Meyer-Rochow, 1973, 1975).

Scarab adults, *Melontha vulgaris* F. (Kirchoffer, 1908), *Oryctes rhinoceros* (Bugnion and Popoff, 1914), and others (Grenacher, 1879) also have scotopic A functional eyes. Based on research on *Repsimus manicatus* Lea (Scarabaeidae) adults, Horridge and Giddings (1971) define the "neuropteran" type of compound eye as having a crystalline thread in the light-adapted state only, with retinula cell bodies extending to the tip of the cone only in the dark-adapted state. Eyes of *Anoplognathus pallidicollis* Blanch (Scarabaeidae) are also scotopic A and have a basal retinula cell (Meyer-Rochow and Horridge, 1975). Although dark and light adaptation experiments here were performed on scotopic A eyes only of *Cicindela lepida*, it is possible to assume that eyes of *Amblycheila schwarzi*, *Megacephala carolina* and *Cicindela lepida* adults are also of the neuropteran type. (*sensu* Horridge and Giddings, 1971). Evolution of a clear retinula zone in these cicindelid eyes is probably an adaptation to permit a further increase in sensitivity in the dark-adapted state by allowing an increase in the acceptance angle of lenses and in the cross-sectional area of the rhabdoms without prejudice to acuity of the light-adapted eye. Optical mechanisms of summation of scattered light in clear zone compound eyes are reviewed by Horridge, 1971; Kunze, 1972; Horridge *et al.*, 1972; Diesendorf and Horridge, 1973; and Horridge, 1975.

Scotopic B eyes

Like eyes of adults of the closely-related genus *Amblycheila* sp. in the same subtribe Omina, scotopic B eyes of *Omus californicus* adults are eucone and have a thick dioptric apparatus and a crystalline thread, but importantly, they have no clear retinula zone. Instead, the rhabdom extends the

full length of the retinula from the distal seventh rhabdomere to the eighth basal retinula cell. Although adephagans usually have a neuropteran type of scotopic eye as defined by Horridge and Giddings (1971), these authors state that some adephagan eyes have long fused rhabdoms. In longitudinal section, ommatidia of *Pterostichus melanarius* (this study), *Procrustes coriaceus* L., *Carabus glabratus* Payk., and *Broscus cephalotes* L. (Carabidae) (Kirchoffer, 1908) also have broad fused rhabdoms and no clear retinula zones. Dorsal and ventral divided eyes of *Gyrinus nator subtritus* Steph., (Bott, 1928), *Gyrinus subtritus*, (Wachmann and Schröder, 1975), *Gyrinus natator* L., (Burghause, 1976), and dorsal eyes of *Dineutes assimilis* adults, (Gryinidae) (Pappas and Larsen, 1973) are also of the scotopic B functional category.

Photopic eyes

Other adult carabid eyes have rhabdoms extending the full retinula length (Bernard, 1932; Home, 1976) These eyes have three levels of rhabdom organization similar to those of *Dytiscus marginalis* adult eyes (Horridge, 1969). However, like eyes of *Omus californicus* adults, there is no clear retinula zone but, importantly, the rhabdoms have less surface area.

A greater reduction of rhabdomeric surface area and volume occurs in photopic eyes of diurnal cicindelid adults of the genus *Cicindela*. From histological examination of adult eyes of diurnal *Cicindela campestris* L., *Cicindela silvatica* Latr., and *Cicindela hybrida* L., Kirchoffer (1905) made descriptions and in 1908 figured ommatidia of the first two species. Further examination of eyes of *Cicindela campestris* by Friedrichs (1931) and Home (1976) confirmed the slender fused rectangular rhabdom structure. Swiecinski (1957) reported a similar retinula organization in eyes of *Cicindela hybrida* adults, and I have also observed this cellular organization in eyes of adults of the following diurnal cicindelids. *Cicindela tranquebarica* Herbst, *Cicindela belfragei* Sallé, *Cicindela limbalis* Klug, *Cicindela longilabris* Say, *Cicindela limbata nympha* Casey, and *Cicindela repanda repanda* Dejean. Since these ommatidia do not have a clear retinula zone or a broad fused rhabdom, light is not scattered over adjacent rhabdoms and the eyes are photopic. Eyes of *Elaphrus americanus* also are photopic and although *Elaphrus cupreus* Duftschmid are active in the shade they have photopic eyes (Kirchoffer, 1908; Bauer, 1974; and Home, 1976) as do heliophilus adults of *Elaphrus riparius* Linnaeus (Bauer, 1974). Possibly, photopic eyes have a greater spectral sensitivity than scotopic eyes (review: Menzel, 1975) and have the ability to detect polarized light (reviews: Snyder, 1973; Wehner, 1976).

Pigment cells

In dark-adapted scotopic A eyes of *Amblycheila schwarzi* adults, pigment is concentrated in distal portions of the secondary pigment cells surrounding the crystalline cones and retinulae extend to the cone tips. The clear retinula zone is devoid of pigment, allowing light to be scattered on adjacent rhabdoms for increased light intensity. Such a cellular organization corresponds to the dark-adapted scotopic eye of the neuropteran type (*sensu* Horridge and Giddings, 1971). Light-adapted scotopic A eyes of *Megacephala carolina* and *Cicindela lepida* have crystalline threads to direct light to individual rhabdoms, but the long clear zones are not surrounded by secondary pigment granules which suggests that light is scattered over adjacent rhabdoms. Dark-adapted photopic B eyes of *Omus californicus* and *Pterostichus melanarius* and light-adapted photopic eyes of *Cicindela tranquebarica*, *Cicindela belfragei* and *Elaphrus americanus* adults have distal aggregations of pigment granules surrounding crystalline cones and threads. Like photopic eyes of *Apis mellifica* L. (Kolb and Autrum, 1972), *Cicindela tranquebarica* and *Cicindela belfragei* eyes also have pigment granules along the retinula length. As postulated for these apid eyes (Varela and Wiitanen, 1970), I suggest that parallel light entering photopic cicindelid and carabid eyes is directed to the rhabdom for phototransduction and

oblique rays are absorbed at the level of the dioptric apparatus by secondary pigment granules. Optical isolation at the retinula level is maintained by an envelope of pigment along its length which prevents stimulation of the rhabdom by light coming from adjacent ommatidia. This presumably results in finer resolution of the image.

Large pigment aggregations on the ventral aspect of the lamina ganglionaris and medulla interface are postulated to be remnants of six larval stemmata similar to that in other adult insect eyes (Weber, 1933). To prove this, an analysis of tissue organization of the pharate pupa would be required. Functionally, this pigment and glial cell pigment may prevent stimulation of the retinula by light entering the eye antidromically through thin cuticular regions.

Retinula cell axons

I did not determine from light microscope studies if axons of similar colour sensitivity in an axonal bundle synapse in the lamina cartridge as observed by Braitenberg (1967) in eyes of *Musca domestica* Meig. (Muscidae). Why the axons are comparatively longer in eyes of *Amblycheila schwarzi* is not understood, but a similar arrangement is also observed in nocturnal scotopic B eyes of *Pterostichus melanarius* and *Steropus madidus* Fab. adults (Carabidae) (Bernard, 1932). Axons of the other cicindelid and carabid beetle eyes are shorter, and these eyes have a lamina, medulla, and lobula broadly similar to photopic eyes of the honey bee *Apis mellifera* L. (Ribi, 1975). To determine exact neural connections, Golgi silver impregnation (Ribi, 1974) of axons and interneurons would be required.

Significance of evolution of character states of cicindelid and carabid beetle compound eyes

In this section, significance of differences in structure and function of compound eyes is approached through a phylogenetic analysis of tiger beetles. This is followed by consideration of taxa representing other families of adephagans. A general pattern is sought and its outlines are explained in terms of the relationship between ecology and diversification.

Also evolution of character states of cicindelid and carabid beetle compound eyes are related to the reconstructed phylogeny (Fig. 61). For readers interested in keys, descriptions and diagnoses of character states of tiger beetle taxa, see Schaupp (1883); Leng (1902, 1920); Bradley (1930); and Arnett (1968). For a discussion of character states determining cleavage points between tribes, see Horn (1908–1915; 1926); Bradley (1930); and Arnett (1968); for subtribes, see Thompson (1857); Horn (1908–1915); Leng (1920); and Wallis (1961); for genera within the subtribe Omina, see Lacordaire (1843); Thompson (1857); Brous (1877); Schaupp (1883); Casey (1897); Leng (1902); Bradley (1930); Arnett (1946, 1968); and Vaurie (1955); the genus *Megacephala*. See Thompson (1857); Schaupp (1883); Horn (1908–1915); Arnett (1946); and Willis (1969); the genus *Cicindela*, see Leconte (1857); Schaupp (1883); Leng (1902, 1920); Horn (1908–1915); Bradley (1930); Arnett (1946, 1968); Rivalier (1954); Wallis (1961); and Willis (1968).

Ancestral stock of the Cicindelidae was probably related to Carabini of the family Carabidae. These primitive cicindelids invaded an ecological zone probably involving hunting of relatively large, active, heavily sclerotized prey, and larvae seizing prey from a fixed hiding place. Adults were probably nocturnal hunters and basically ground beetle-like in behaviour. They did not fly actively. Early divergence produced two lines, one retained the plesiotypic small, scotopic A eyes and nocturnal behaviours (the Megacephalini); the other acquired large eyes (ancestors of the Cicindelini).

Within the Megacephalini, two major lineages developed; the Omina, whose adults retained small eyes, and mainly nocturnal behaviour; and the Megacephalina, whose adults became crepuscular acquired large eyes for stereopsis, but remained functionally scotopic A. Within the Omina, adults are secondarily flightless. Adults of *Amblycheila* plesiotypically have small scotopic A eyes. However, eyes

of *Omus* adults have evolved scotopic B eyes capable of finer image resolution for vision during more frequent diurnal activity periods.

The Cicindelini became divergent and probably initially diversified in the shade of tropical forests, where representatives of many cicindelid genera now live. Early lineages moved into more open areas (initially, perhaps, along stream margins), developed quick flight, which could have been a correlate of the superior binocular vision afforded by large eyes. A lineage with such properties could have been ancestral to *Cicindela*, whose species became diurnal, and adapted for life in open areas. This taxon underwent an evolutionary flowering that produced an abundance of species on all continents (except Antarctica).

Among the species of *Cicindela* I examined, I found two functional eye types: plesiotypic scotopic A; and apotypic photopic. Given only this information, one would be tempted to think that the taxa with scotopic A eyes were ancestral to those with photopic eyes. However, I believe that the reverse is true, based on the following consideration. Photopic eyes and diurnal activity are characteristic of groups possessing more primitive male genitalia, and hence believed to represent more primitive lineages of the genus. These species and the groups to which they belong (indicated by numbers in Freitag, 1974), based on Rivalier, (1954) are: group 1A – *Cicindela repanda* and *Cicindela limbata*; Group 1B – *Cicindela longilabris*; Group 1C – *Cicindela limbalis*; Group III – *Cicindela tranquebarica*. On the other hand, adults of some taxa characterized by highly derived genitalia are crepuscular as well as diurnal, and have either photopic or scotopic A eyes. These are: Group X – *Cicindela belfragei*, eyes photopic; Group XII – *Cicindela lepida* eyes scotopic A. Adults of *Cicindelida pilatei* (Group X) and *Cicindelida lemniscata* (Group XI) are active both in full light and in dim light, but their eyes have not been examined histologically.

Because of the nature of the correlations, I infer that diurnal activity and photopic eyes are plesiotypic in *Cicindela*, and that crepuscular activity and scotopic A eyes are apotypic. Therefore, presence of the latter type of eyes in *Cicindela* represents an evolutionary reversal.

Basically this phylogenetic framework provides a satisfactory continuity of evolution of eye function through nocturnal to crepuscular, and diurnal to crepuscular diel activity transitions. However, one abrupt change from nocturnal to diurnal is involved in the divergence of the Cicindelini from the Megacephalini. It must be mentioned that within the Cicindelini there are four subtribes containing a total of 16 genera which are more primitive than *Cicindela* (Horn, 1926). Eyes of adults of these genera may provide a smooth transition from ancestral small scotopic A eyes through large scotopic A eyes to still larger photopic eyes of *Cicindela* adults.

Based on earlier classification (Lacordaire, 1843, 1854; and Thompson, 1857), an alternative reconstructed phylogeny can be provided. This places the crepuscular Megacephalina as the sister group of the diurnal Cicindelini. One can then propose that the ancestors of these two taxa were crepuscular, like the extant members of the Megacephalina. Thus a smooth transition is provided for evolution of photopic eyes as suggested above. I believe that Horn's hypothesis is more correct and suggest that in the strict sense ancestors of Cicindelini had crepuscular eyes. This hypothesis should be tested by examination of eyes of the more primitive taxa of Cicindelini.

Using Horn's classification, several assumptions are required for the following events of evolution of cicindelid compound eyes: divergence in eye size; divergence in eye function; divergence in eye size and function; parallel acquisition of enlarged eyes; and reversion in function (but not in eye size) to an ancestral condition. Divergence in eye size alone is exhibited by evolution of large eyes in the Megacephalina; divergence in function alone, by acquisition of scotopic B eyes in adults of *Omus*; divergence in eye size and function by evolving eyes of ancestral Cicindelini. Parallel evolution of eye size is exhibited by independent acquisition of large eyes in both Megacephalina and Cicindelini.

Reversal in function is exhibited by evolution of scotopic A eyes by a highly derived lineage of *Cicindela lepida*. Also, in highly derived *Cicindela belfragei*, there is a reversal from diurnal to crepuscular diel activity, without change in eye function.

Table 7 shows that, based on my three functional categories, cellular organization in adepagan beetle eyes has undergone parallel evolution. Parallelism in function is identified in independent acquisition of scotopic B eyes among Cicindelidae (*Omus* spp.), Carabidae (*Pterostichus melanarius*

Table 7. Functional eye categories of adepagan beetle adults.

Family	Functional Eye Category	References
Cicindelidae	Scotopic A	this paper
	Scotopic B	this paper
	Photopic	Kirchoffer, 1905; 1908 Friedrichs, 1931 Swiecinski, 1957 Home, 1976 this paper
Carabidae	Scotopic A	Kirchoffer, 1905; 1908 Bernard, 1932 Hasselmann, 1962
	Scotopic B	Grenacher, 1879 Kirchoffer, 1905; 1908 Bernard, 1932 this paper
	Photopic	Kirchoffer, 1905; 1908 Horridge and Giddings, 1971a Bauer, 1974 Home, 1976 this paper
Dytiscidae	Scotopic A	Grenacher, 1879 Exner, 1891 Kirchoffer, 1905; 1908 Horridge, 1969a Horridge <i>et al.</i> , 1970 Meyer-Rochow, 1973; 1975
Gyrinidae	Scotopic B	Kirchoffer, 1905; 1908 Horridge and Giddings, 1971a Pappas and Larsen, 1973 Wachmann and Schröer, 1975 Burghause, 1976

and other taxa), and Gyrinidae (*Gyrinus* spp.). Parallelism in eye size and function related to diurnal activity is shown by Cicindelidae (*Cicindela* spp.) and Carabidae (*Elaphrus* spp.). All families but Gyrinidae have living taxa with ancestral scotopic A eyes. The impression is that parallel acquisition of the derived types of eyes occurred many times. Reversion to an ancestral functional condition might be common, though probably less frequent than parallelism.

It is important to recapitulate that modifications are based on eye size and on an alteration of cellular organization not on a change in cell number in ommatidia. Coadapted to nocturnal activity are small scotopic A eyes, scotopic B eyes to nocturnal but more frequent diurnal activity; to crepuscular activity, large scotopic A eyes (except large photopic eyes of *Cicindela belfragei*); and to diurnal activity, large photopic eyes.

The mechanism used to evolve large eyes from small eyes is addition of number of ommatidia with an accompanying shortening of the dioptric apparatus and increased retinula length. The transition from scotopic A to scotopic B eyes involves elimination of the clear retinula zone by extension of the rhabdom the complete retinula length. Such a structural modification only involves shortening of the retinula cells. Changes involved with elimination of the clear retinula zone and reduction of rhabdom surface area and volume, evolve photopic eyes from large scotopic A eyes, and converse relationships are required for the opposite transition.

Because slight changes in internal structure have profound effects on function, it is fairly easy for evolving groups to move from one adaptive zone to another, and back again. Such shifts are generally correlated with speciation. This means an increase in diversity when such shifts occur, and ultimately they involve change in eye function. Therefore, it seems likely that the ability of eyes to respond quickly to selection is an integral component of evolution of diversity among the Adephaga in particular, and perhaps among insects in general.

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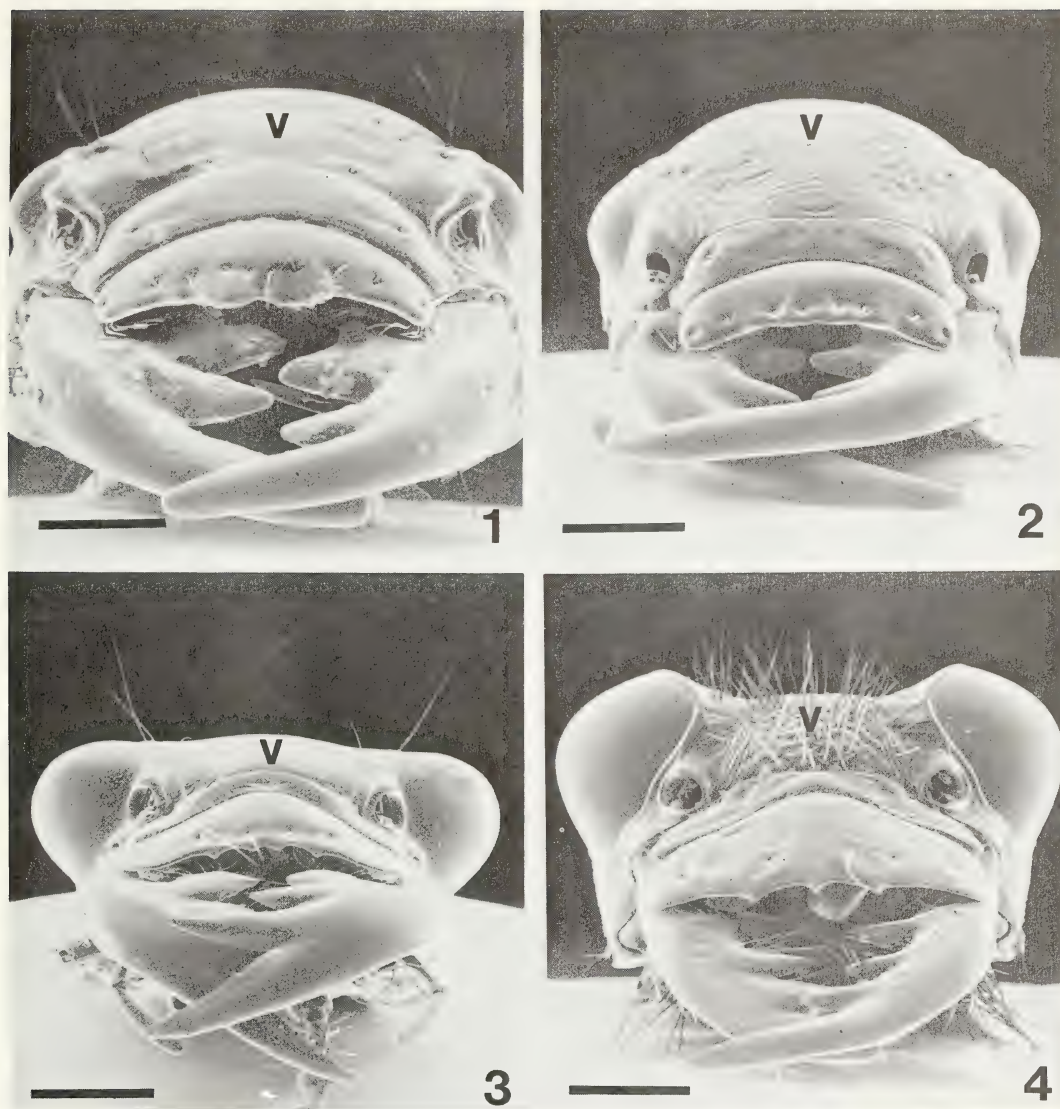
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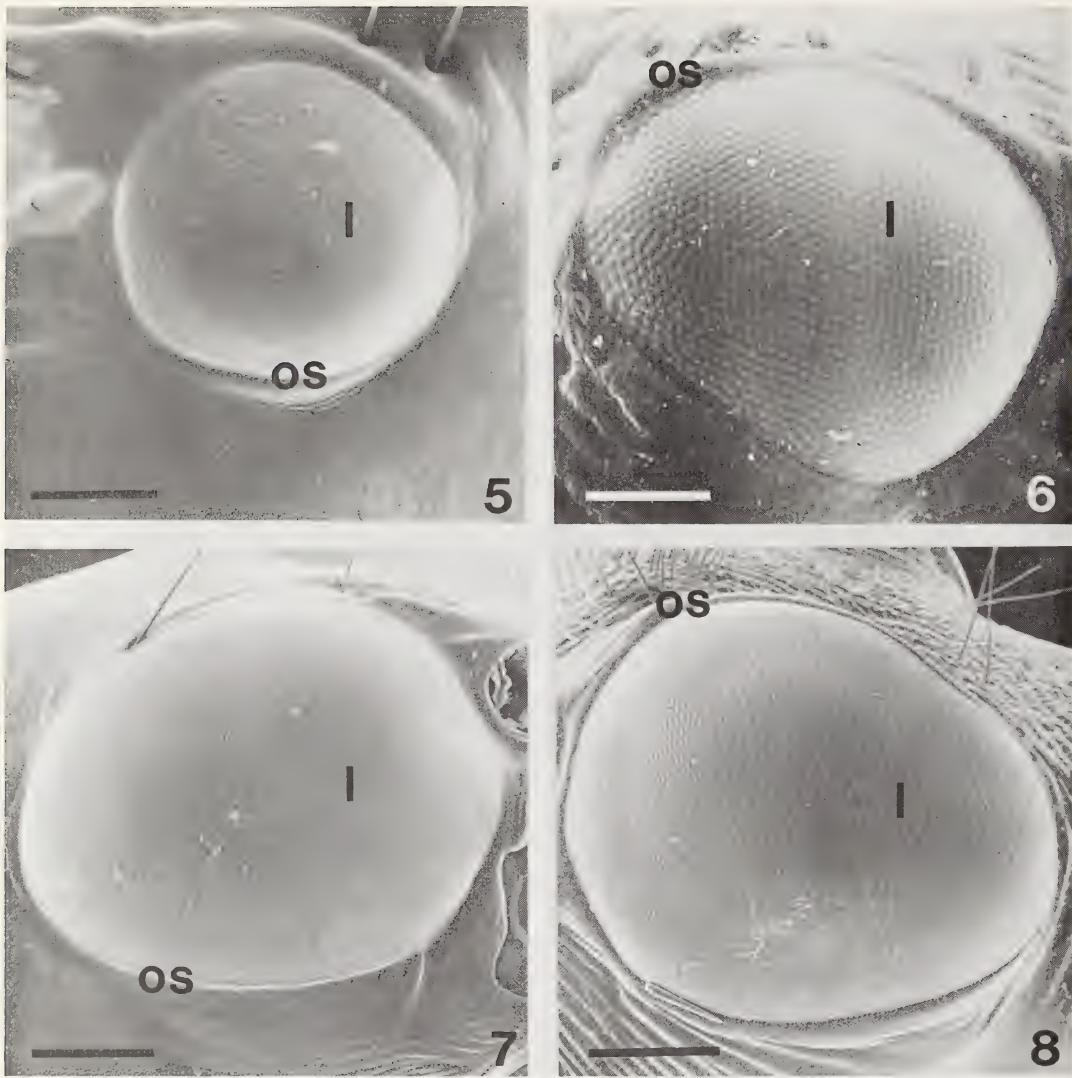
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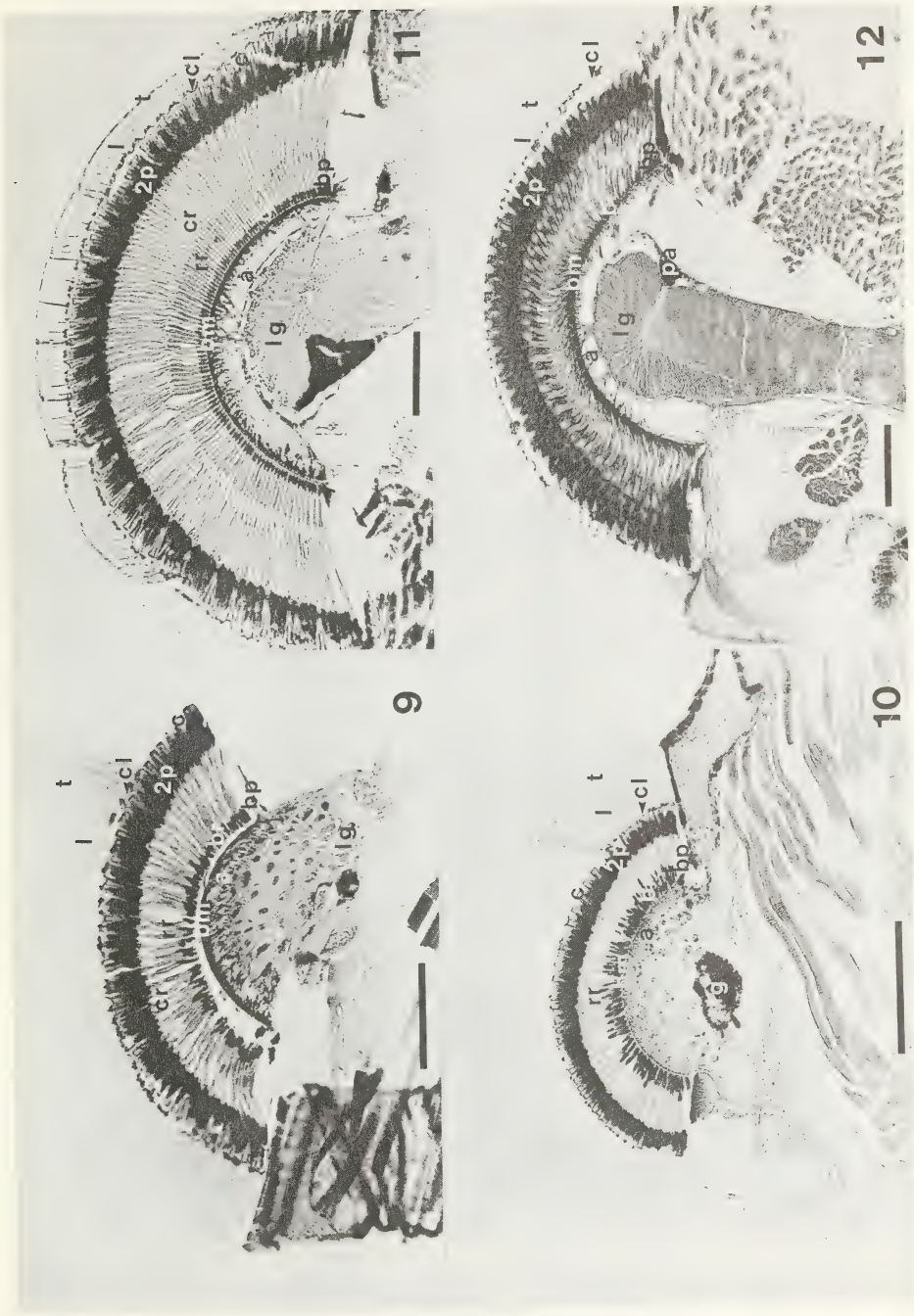
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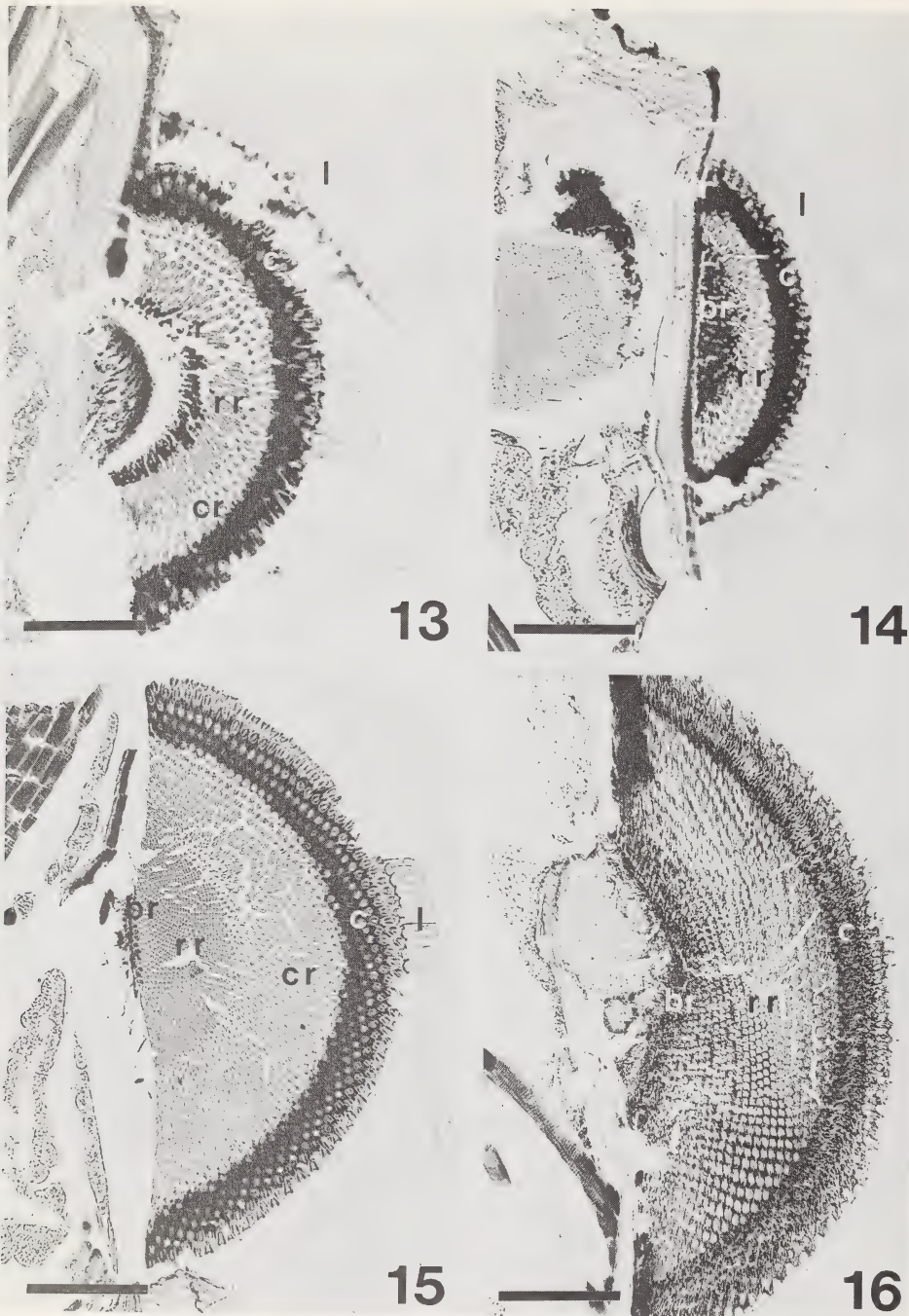
Figures 1 – 4. SEM of the frontal aspect of heads of cicindelid beetles, showing variation in eye size and shape. Note vertexes (v). Scale = 500 μ m.



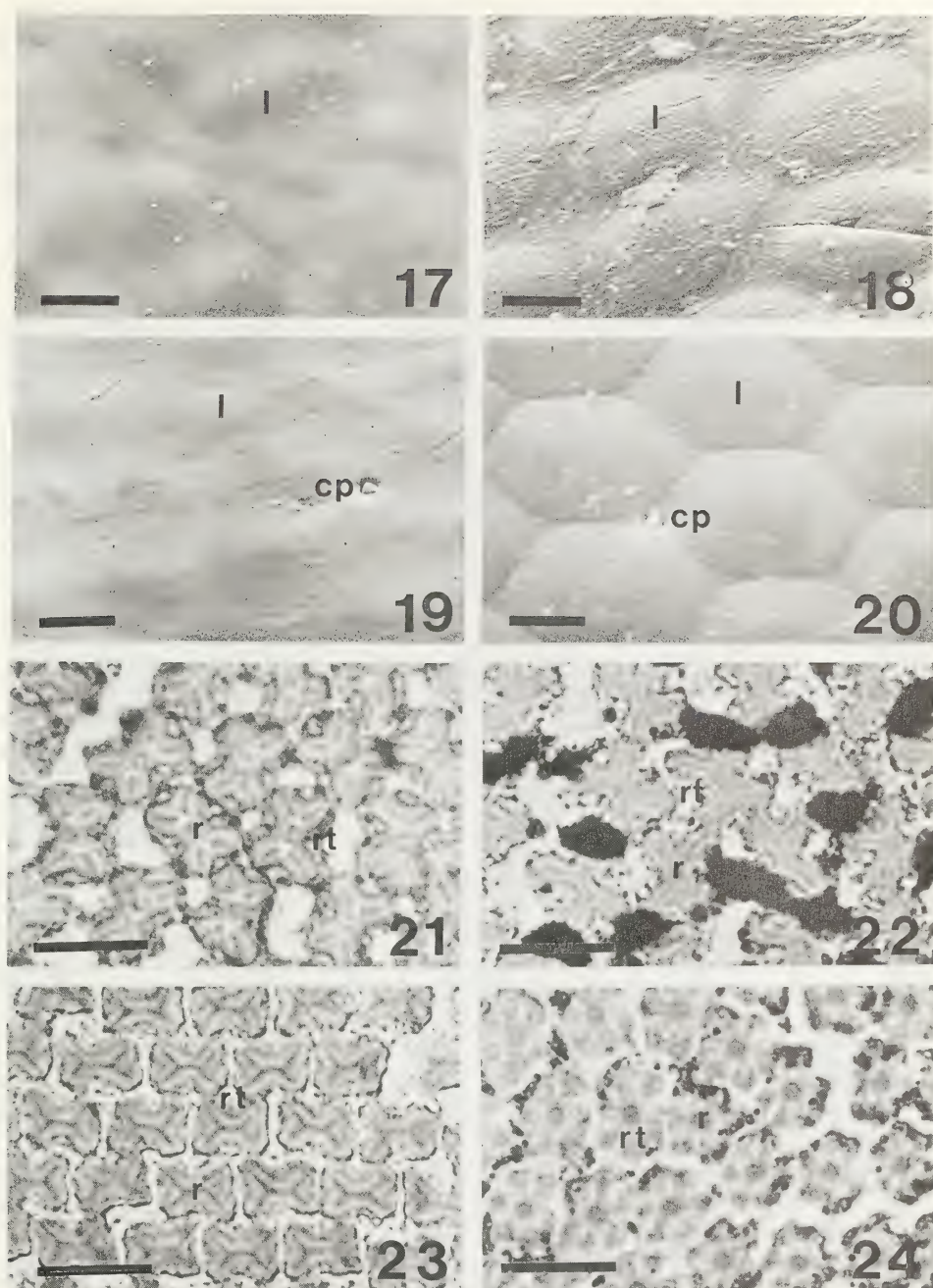
Figures 5–8. Lateral view of compound eyes of cicindelid beetles, showing hexagonal corneal lenses (l) and ocular sclerite (os). Scale = 200 μ m. Fig. 1,5: *Amblycheila schwarzi*; Fig. 2,6: *Omus californicus*; Fig. 3,7: *Megacephala carolina*; and Fig. 4,6: *Cicindela tranquebarica*.



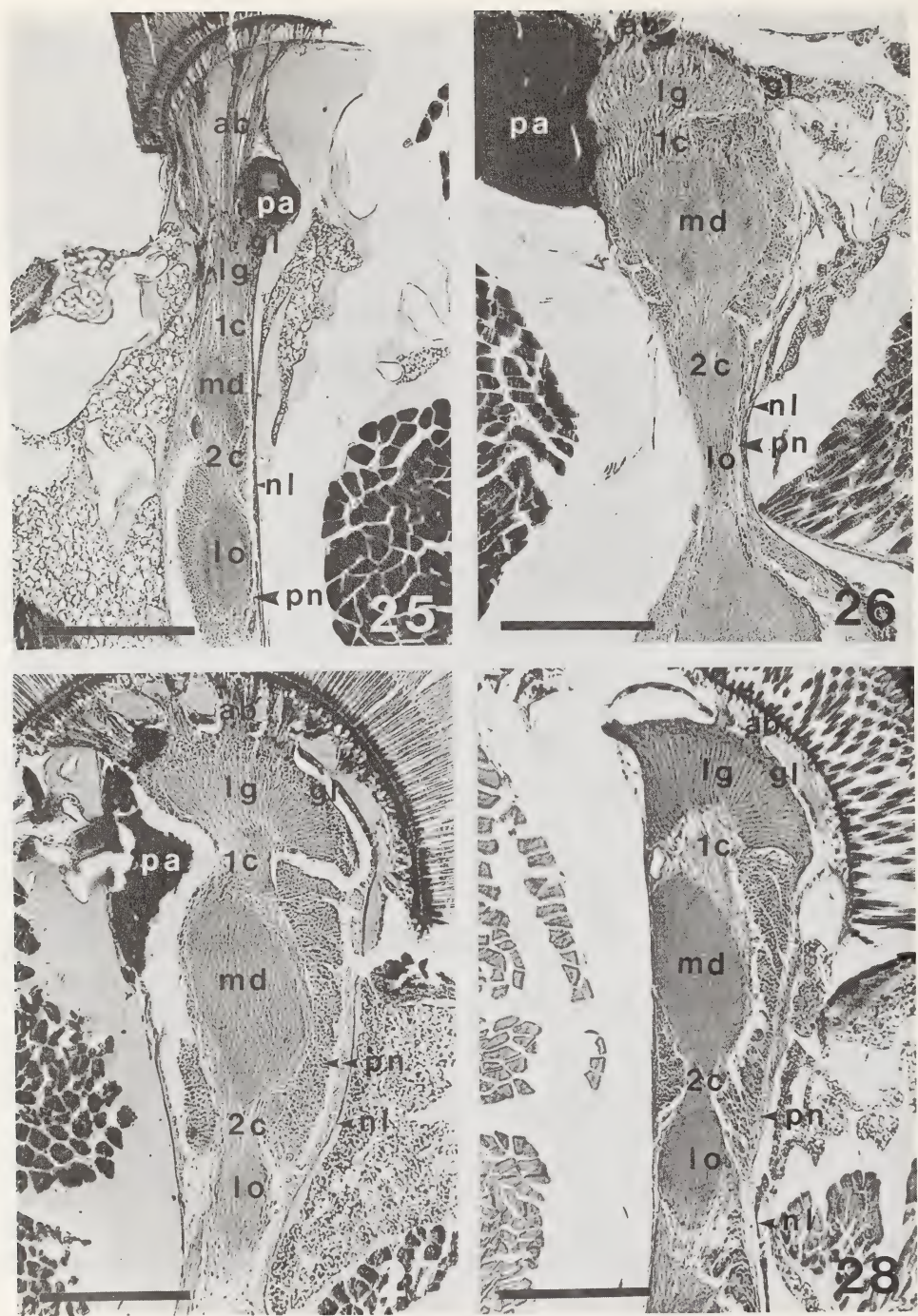
Figures 9 – 12. LM of longitudinal sections of compound eyes of cicindelid beetles. Shown are: thin corneal layer (tl); corneal lens (l); corneal layer (cl); crystalline cone (c); clear retinula zone (cr); retinula rhabdom zone (rr); basal retinula zone (br); basement membrane (bm); secondary pigment cells (2p); basal pigment cells (bp); axons (a); and lamina ganglionaris (lg). Scale = 200 μ m. Fig. 9: *Amblycheila schwarzi*; Fig. 10: *Omus californicus*; Fig. 11: *Megacephala carolina*; Fig. 12: *Cicindela tranquebarica*.



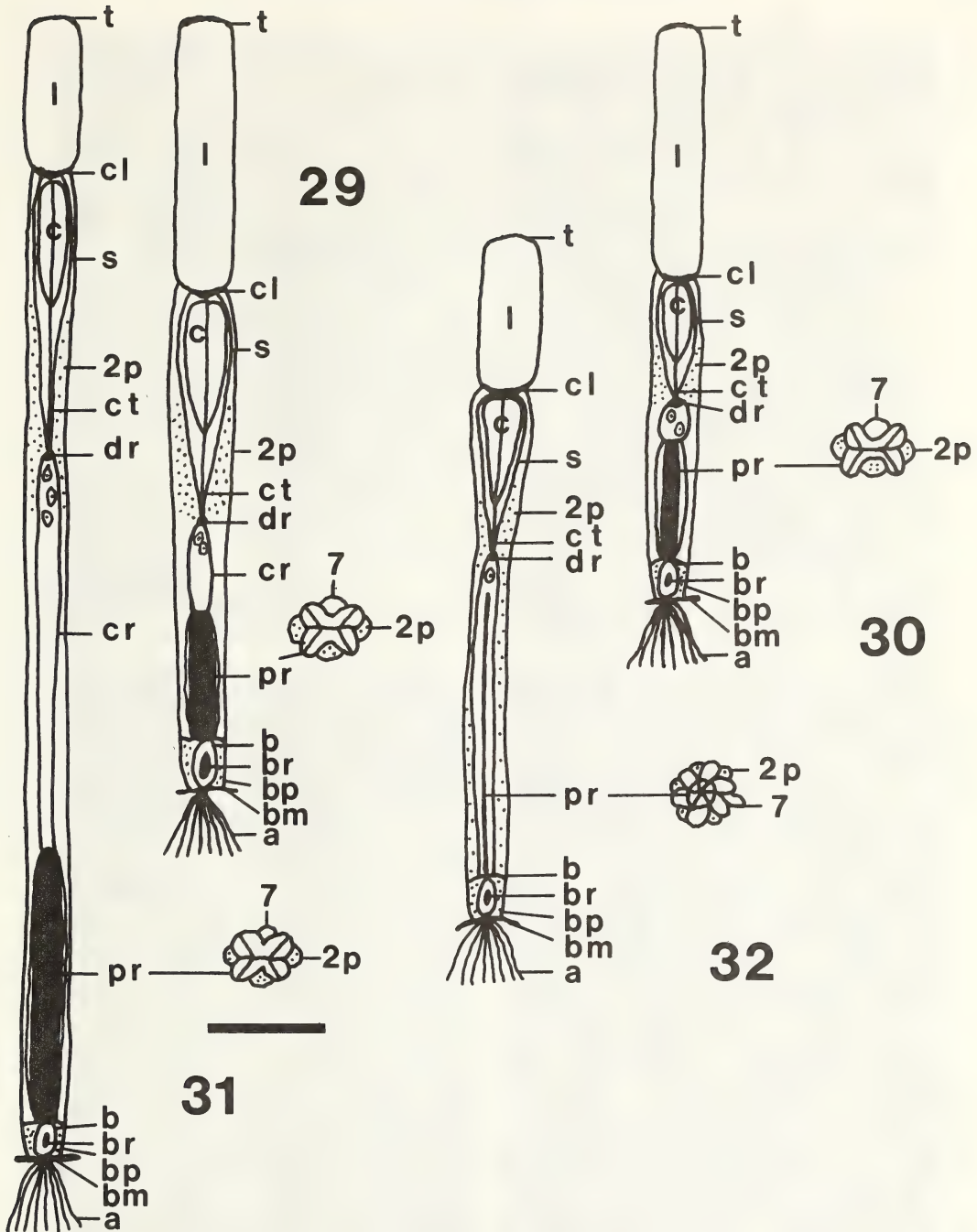
Figures 13 – 16. LM of transverse sections of compound eyes of cicindelid beetles. Structural component abbreviations as in Fig. 9–12. Scale = 100 μ m. Fig. 13: *Amblycheila schwarzi*; Fig. 14: *Omus californicus*; Fig. 15: *Megacephala carolina*; and Fig. 16: *Cicindela tranquebarica*.



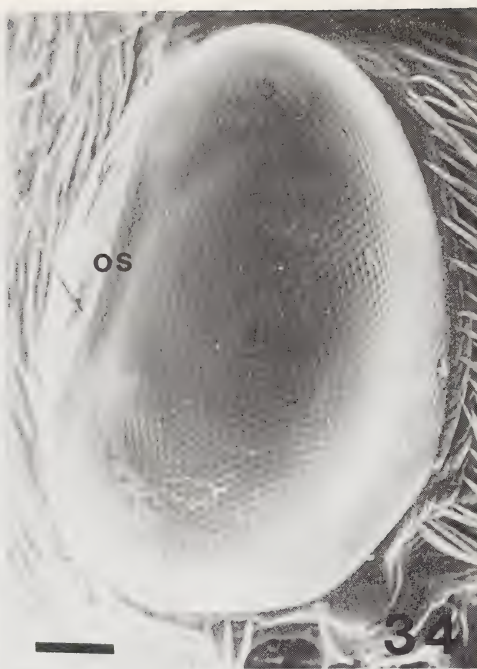
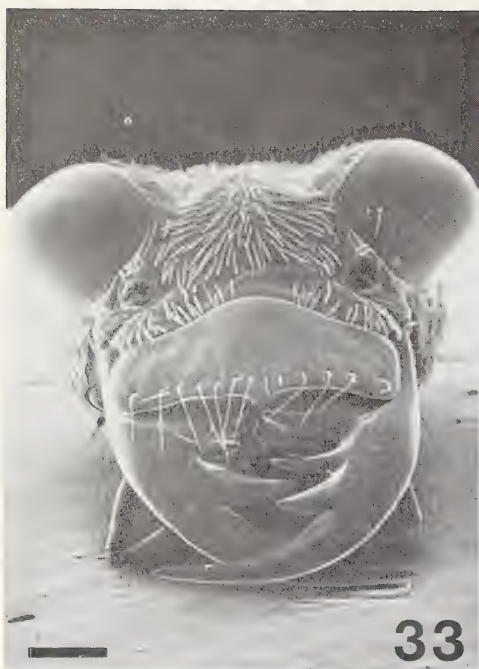
Figs. 17 – 24. SEM of convex, hexagonal corneal lenses (l) of cicindelid beetles. Note cuticular pegs (cp) between some lenses. Scale = 10 μ m. Figures 21 – 24. LM of transverse sections through the retinula cells (rt) and rhabdom (r). Scale = 20 μ m. Fig. 17,21: *Amblycheila schwarzi*; Fig. 18,22: *Omus californicus*; Fig. 19,23: *Megacephala carolina*; and Fig. 20,24: *Cicindela tranquebarica*.



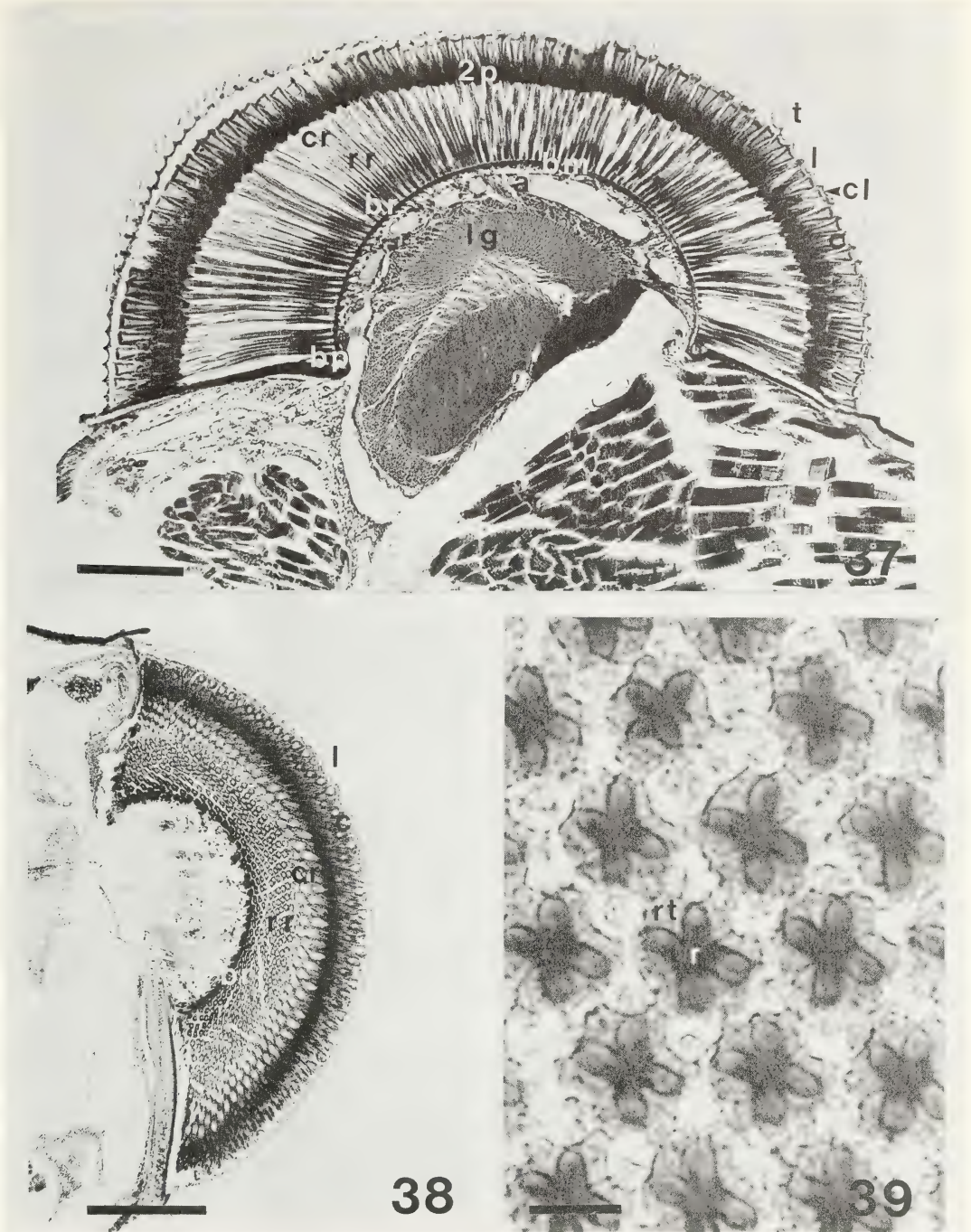
Figures 25 – 28. Frontal sections through optic lobes of cicindelid beetles, showing axonal bundles (ab); glial cells (gl); lamina ganglionaris (lg); first optic chiasmata (lc); medulla (md); second optic chiasmata (2c); lobula (lo); neurilemma (nl); and perineurium (pn). Note dense pigment accumulation (pa) on the ventral aspect of optic lobes. Scale = 100 μ m. Fig. 25: *Amblycheila schwarzi*; Fig. 26: *Omus californicus*; Fig. 27: *Megacephala carolina* ; Fig. 28 *Cicindela tranquebarica*.



Figures 29 – 32. Diagrammatic longitudinal sections of representative ommatidia and transverse sections of proximal rhabdoms of four cicindelid beetles, showing thin corneal layer (t); corneal lens (l); subcorneal layer (cl); crystalline cone (c); Semper cells (s); crystalline thread (ct); distal rhabdom (dr) of retinula cell seven (7); clear retinula zone (cr); proximal rhabdom (pr) of six retinula cells; basal retinula cell (b) with rhabdomere (br) secondary pigment cells (2p); basal pigment cells (bp); basement membrane (bm); and eight axons (a). Longitudinal section scale = 50 μ m. Transverse section scale = 20 μ m. Fig. 29: *Amblycheila schwarzi* (scotopic A); Fig. 30: *Omus californicus* (scotopic B); Fig. 31: *Megacephala carolina* (scotopic A); and Fig. 32: *Cicindela tranquebarica* (photopic).



Figures 33 – 36. SEM of the frontal aspect of the head of a *Cicindela lepida* adult, showing large bulbous eyes. Scale = 500 μ m. Fig. 34. Same, of a lateral view of the left compound eye, showing hexagonal corneal lenses (l) and ocular sclerite (os). Vertex positioned at the left. Scale = 200 μ m. Fig. 35. Same, of convex distal surfaces of hexagonal corneal lenses (l). Note cuticular pegs (cp) between some lenses. Scale = 10 μ m. Fig. 36. Same, of a cuticular peg (cp) of an interfacetal mechanoreceptor. Note ecdysial scar (es). Scale = 1 μ m.



Figures 37 – 39. LM of longitudinal section of the eye of a *Cicindela lepida* adult. Shown are: thin corneal layer (t); corneal lens (l); subcorneal layer (cl); crystalline cone (c); clear retinula zone (cr); retinula rhabdom zone (rr); basal retinula zone (br); basement membrane (bm); secondary pigment cells (2p); basal pigment cells (bp); axons (a); and lamina ganglionaris (lg). Scale = 100 μ m. Fig. 38. LM of transverse section of the eye. Structural component abbreviations as above. Scale = 200 μ m. Fig. 39. Same, through the retinula rhabdom zone, showing retinula cells (rt) and rhabdom (r). Scale = 10 μ m.

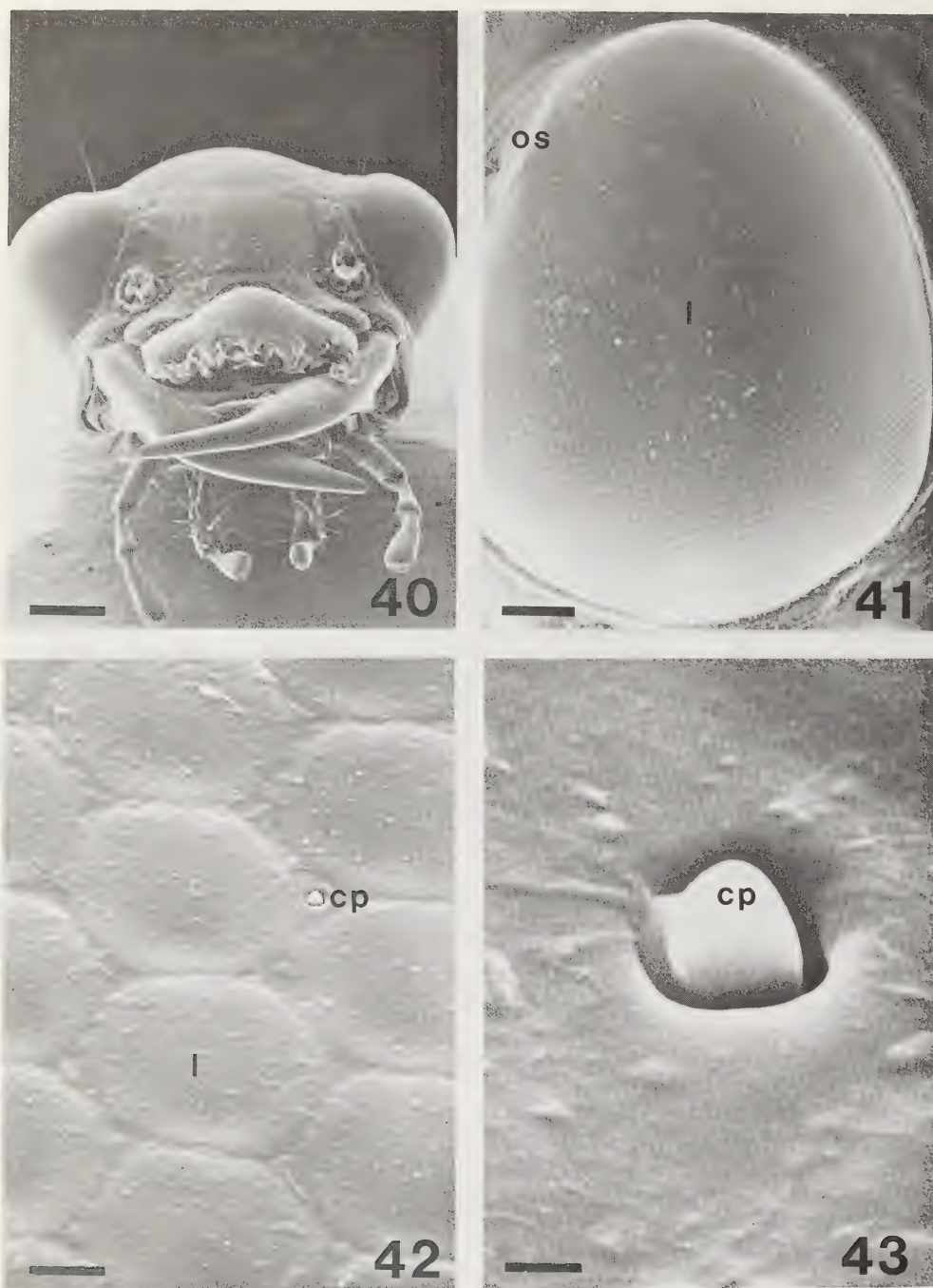


Figure 40 – 43. SEM of the frontal aspect of the head of a *Cicindela belfragei* adult, showing large bulbous eyes. Scale = 500 μ m. Fig. 41. Same, of a lateral view of the left compound eye, showing hexagonal corneal lenses (l) and ocular sclerite (os). Vertex positioned at the left. Scale = 200 μ m. Fig. 42. Same, of convex distal surfaces of hexagonal corneal lenses (l). Note cuticular pegs (cp) between some lenses. Scale = 10 μ m. Fig. 43. Same, of a cuticular peg (cp) of an interfacetal mechanoreceptor. Scale = 1 μ m.



Figure 44 – 46. LM of longitudinal section of the eye of a *Cicindela belfragei* adult. Shown are: thin corneal layer (t); corneal lens (l); subcorneal layer (cl); crystalline cone (c); retinula rhabdom zone (rr); basal retinula zone (br); basement membrane (bm); secondary pigment cells (2p); basal pigment cells (bp); axons (a); and lamina ganglionaris (lg). Scale = 100 μ m. Fig. 45. LM of transverse section of the eye. Structural component abbreviations as above. Scale = 200 μ m. Fig. 46. Same, through the retinula rhabdom zone, showing retinula cells (rt) and rhabdom (r). Scale = 10 μ m.

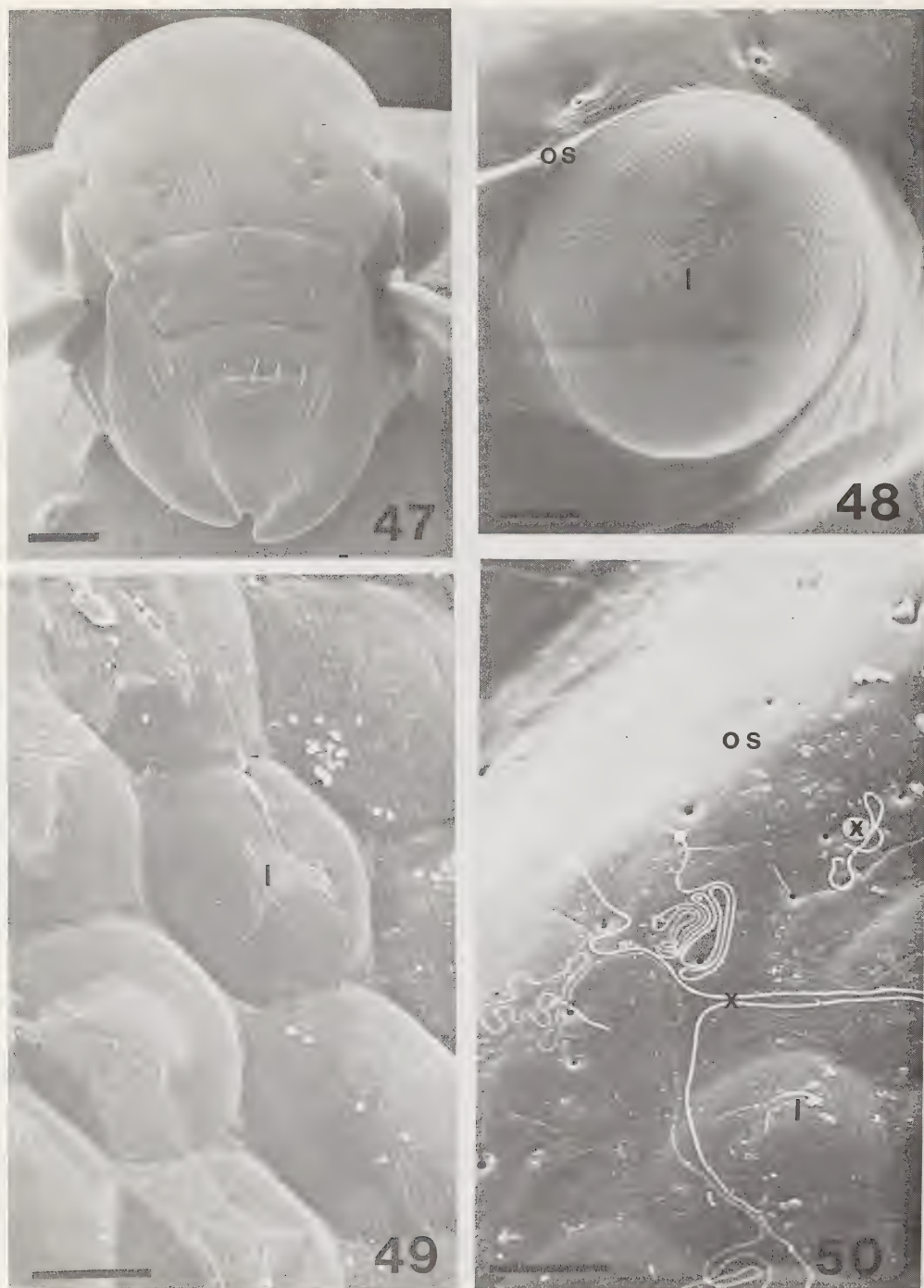
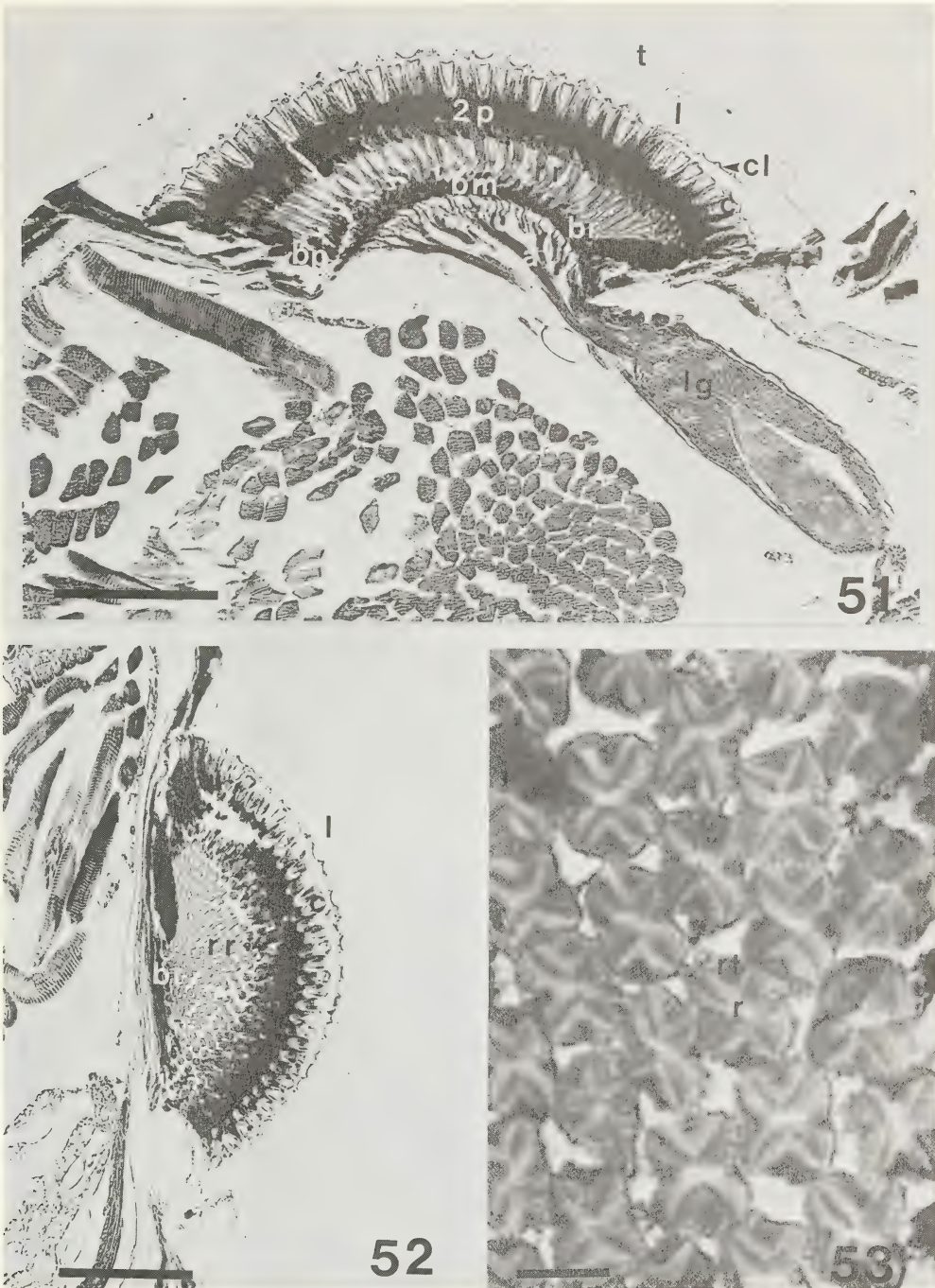
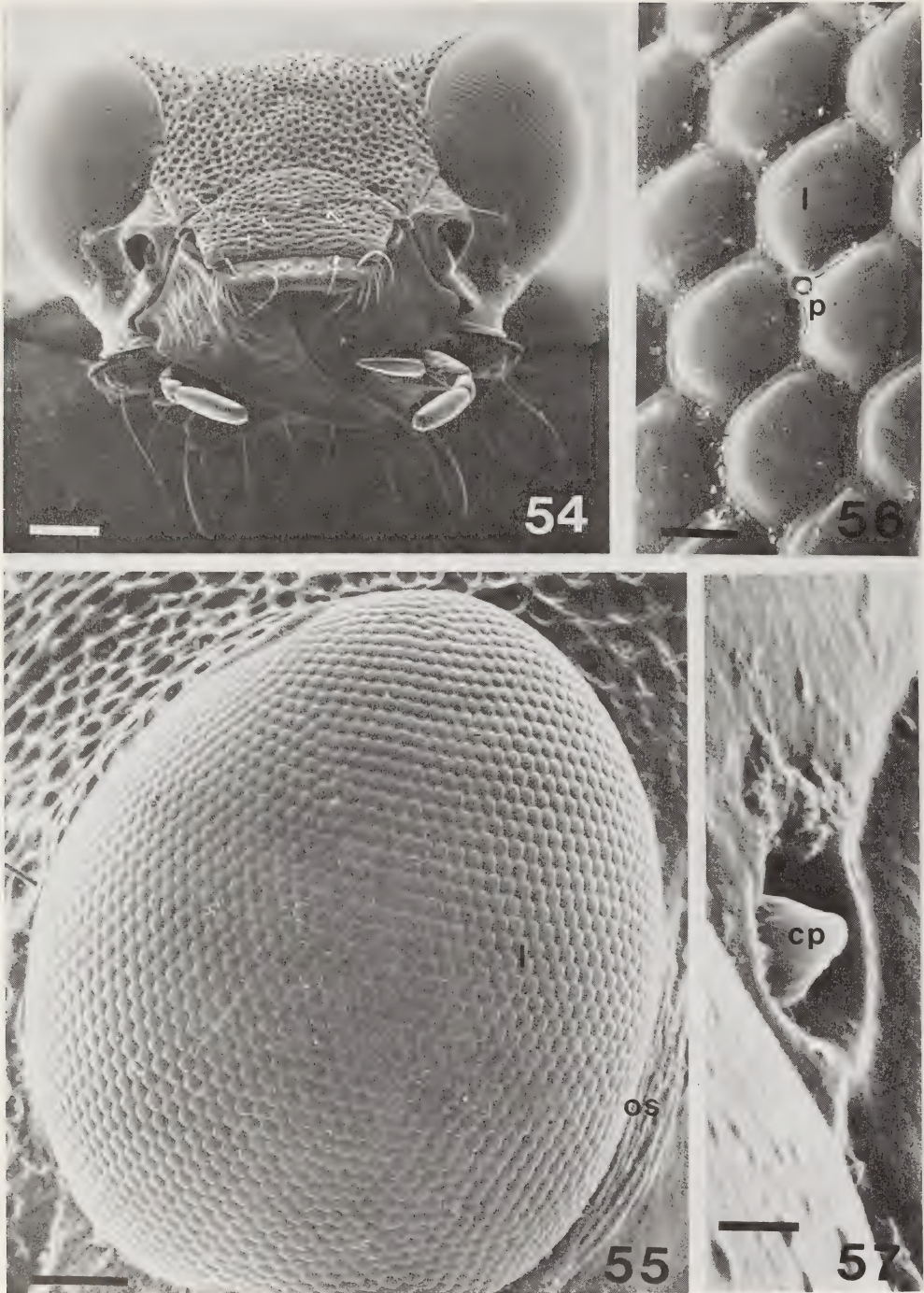


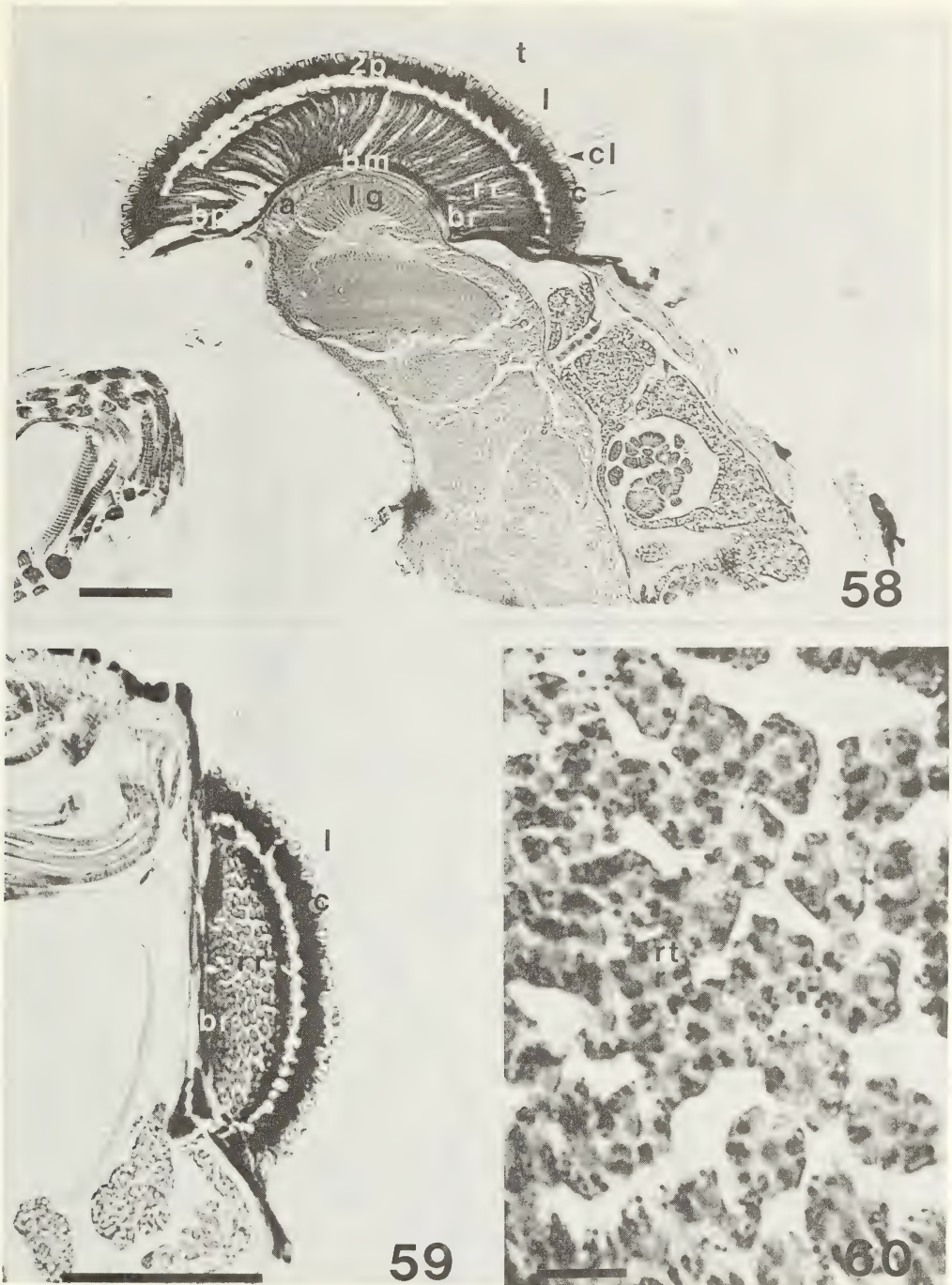
Figure 47 – 50. SEM of the frontal aspect of the head of a *Pterostichus melanarius* adult, showing relatively flat eyes. Scale = 500 μ m. Fig. 48. Same, of a lateral view of the left compound eye, showing hexagonal corneal lenses (I) and ocular sclerite (os). Vertex at the top. Scale = 200 μ m. Fig. 49. Same, of convex distal surfaces of hexagonal corneal lenses (I). No interfacetal pegs are present. Scale = 10 μ m. Fig. 50. Same, of dermal glands surrounding the eye. Glands secrete a material (x) which spreads over the ocular sclerite (os) and some corneal lenses (I). Scale = 10 μ m.



Figures 51 – 53. LM of longitudinal section of the eye of a *Pterostichus melanarius* adult. Shown are: thin corneal layer (t); corneal lens (l); subcorneal layer (cl); crystalline cone (c); retinula rhabdom zone (rr); basal retinula zone (br); membrane (bm); secondary pigment cells (2p); basal pigment cells (bp); axons (a); and lamina ganglionaris (lg). Scale = 100 μ m. Fig. 52. LM of transverse section of the eye. Structural component abbreviations as above. Scale = 100 μ m. Fig. 53. Same, through the retinula rhabdom zone, showing retinula cells (rt) and rhabdom (r). Scale = 10 μ m.



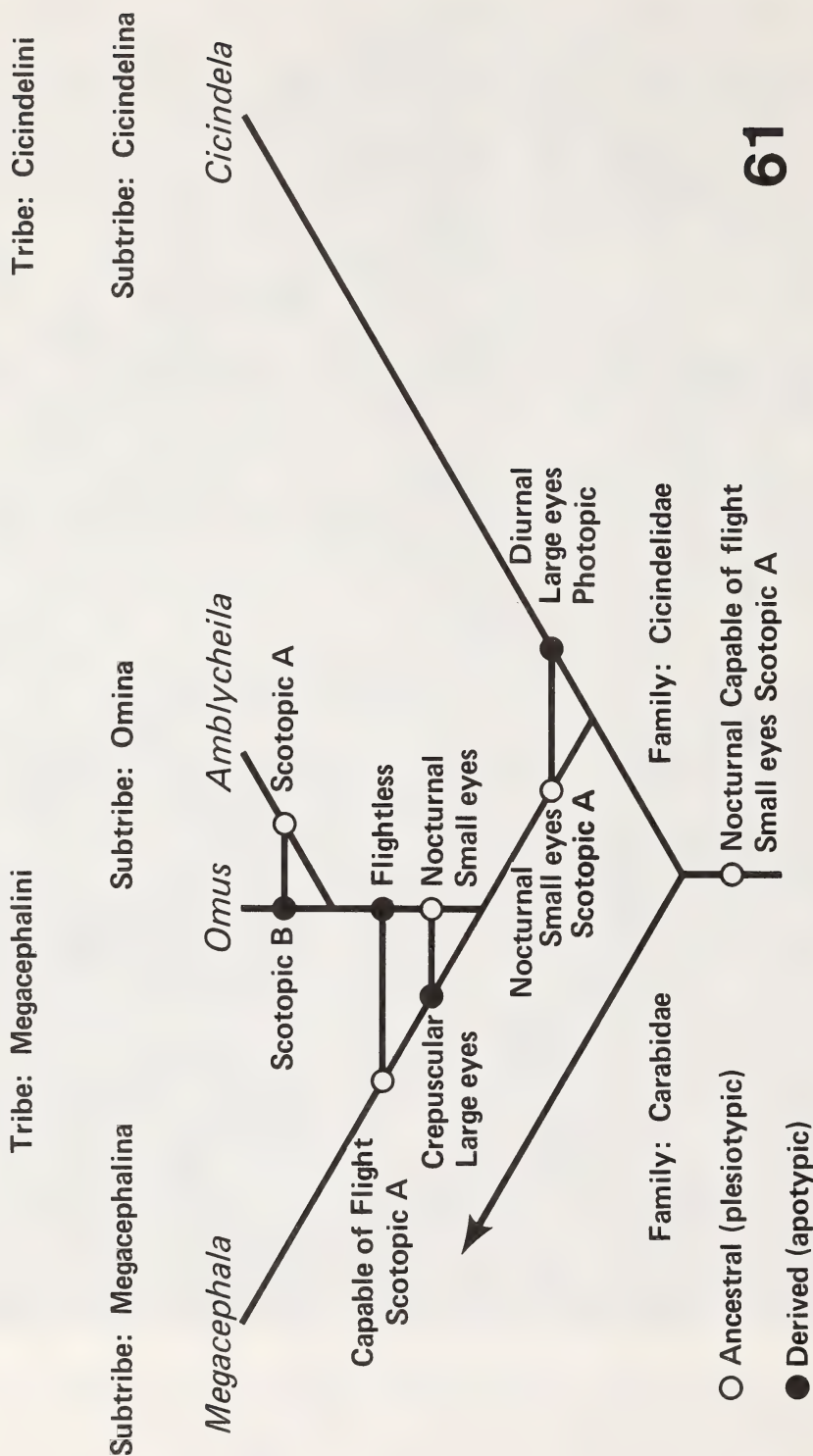
Figures 54 – 57. SEM of the frontal aspect of the head of an *Elaphrus americanus* adult, showing large bulbous eyes. Scale = 200 μ m. Fig. 55. Same, of a lateral view of the left compound eye, showing hexagonal corneal lenses (l) and ocular sclerite (os). Vertex positioned at the left. Scale = 100 μ m. Fig. 56. Same, of convex distal surfaces of hexagonal corneal lenses (l). Note cuticular pegs (cp) between some lenses. Scale = 10 μ m. Fig. 57. Same of a cuticular peg (cp) of an interfacetal mechanoreceptor. Scale = 1 μ m.



Figures 58 – 60. LM of longitudinal section of the eye of an *Elaphrus americanus* adult. Shown are: thin corneal layer (t); corneal lens (l); subcorneal layer (cl); crystalline cone (c); retinula rhabdom zone (rr); basal retinula zone (br); basement membrane (bm); secondary pigment cells (2p); basal pigment cells (bp); axons (a); and lamina ganglionaris (lg).

Scale = 100 μ m. Fig. 59. LM of transverse section of the eye. Structural component abbreviations as above. Scale = 200 μ m. Fig. 60. Same, through the retinula rhabdom zone, showing retinula cells (rt) and rhabdom (r). Scale = 10 μ m.

Reconstructed Phylogeny of North American Genera of Cicindelidae Based on Horn, 1926 and Compound Eye Structure and Function



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Figure 61. Reconstructed phylogeny of North American Cicindelidae (based on Horn, 1926).

INSECT DAMAGE TO OLD OAK BEAMS AT LOWER FORT GARRY, MANITOBA

HORNE R. WONG

Northern Forest Research Centre

Canadian Forestry Service

Environment Canada

Edmonton, Alberta T6H 3S5

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Old oak beams used in construction of ceilings of first and second storeys and lintels of the limestone warehouse, Lower Fort Garry, Manitoba, were attacked by Dermestes lardarius, Priobium sericeum, and Pseudohadrotoma sp. The insects were probably brought in on goods or originated locally.

Les vieilles poutres de chêne utilisées dans la construction des plafonds du premier et du deuxième étages, et des linteaux des entrepôts en pierre à chaux de Lower Fort Garry, Manitoba, ont subi l'attaque de Dermestes lardarius, Priobium sericeum et Pseudohadrotoma sp. Ces insectes furent probablement introduits avec des marchandises, ou bien étaient d'origine locale.

INTRODUCTION

Lower Fort Garry was built 32 km north of Winnipeg after a disastrous flood ruined old Fort Garry (Winnipeg) at the forks of the Red and Assiniboine rivers in 1826 (Goldring, 1970). Construction was started in 1831 and finished in 1847 with completion of the walls surrounding the buildings. In 1963, an extensive restoration of the fort began. In the process of restoring the old warehouse building, H. Van der Putten, Project Manager of Restoration of Lower Fort Garry, observed considerable insect damage (Fig. 6,7) to the old oak beams. Some of the damage resembled that caused by the death watch beetle, *Xestobium rufovillosum* (De Geer), a destructive insect introduced from Europe and known to attack oak timbers in old buildings.

The purpose of this study was to identify the insect species damaging oak beams and speculate on their origin.

THE WAREHOUSE BUILDING

The three-storey limestone warehouse building (Fig. 1), constructed between 1835 and 1845 (Van der Putten, pers. comm.), measures 21 m long and 9 m wide. Oak used for the ceilings of the first and second storeys and lintels over the windows of the warehouse was floated down the Red River to the fort from the United States and areas around the fort (Van der Putten, pers. comm.). The wood was cut into beams measuring 9 m long, 17.5–22.5 cm wide, and 20.0–22.5 cm high; the beams were spaced 60–75 cm apart. The lengths of the lintels varied from 1.8 to 7.2 m.

The building was originally used by the Hudson's Bay Company to house supplies for the fur trade, but it also served several subsequent functions: a barracks for the military (1846–48), the first provincial and later federal penitentiary (1871–77), and Manitoba's first asylum (1885–86) (Goldring 1970). It was while the warehouse was used as a penitentiary that a lime wash, still evident today (Fig. 2), was painted over the beams and lintels (Van der Putten, pers. comm.).

METHODS AND MATERIAL

Infested oak beams from the warehouse were cut into small sections and shipped to the Northern Forest Research Centre in late November 1976. These were split into smaller pieces and examined for insects within the wood. Adults for identification were obtained by placing those pieces containing living larvae in 73.12-liter galvanized metal garbage cans, modified as in Fig. 4. The cans were placed in a rearing room with a temperature of 21 C and relative humidity of 50%. Daily observations were made for adult emergence.

INSECT SPECIES AND DISCUSSION

Three species of insects were found in the oak beams.

Dermestes lardarius Linnaeus

This was the most abundant species present, observed throughout the beams, although rarely in lintels or the spruce floor. All larvae, pupae, and adults in the wood were dead (Fig. 6). Their presence in the oak beams can be attributed to the building having been used to store supplies of the Hudson's Bay Company. Full-grown larvae, which feed on furs, hides, and anything of animal origin, are known to wander about in search of some compact material in which to bore a tunnel to pupate (Hinton 1945). The compact material near at hand was the oak beams and spruce floor. Instances of the larder beetle damaging structural wood are common. Hinton (1945) listed a number of such reports, and Craighead (1950) and Baker (1972) noted that valuable cargos of lumber have been damaged in ship holds where hides had previously been stored.

It is not known for certain what killed the beetles in the wood. A chemical analysis of the dead larvae and adults did not disclose any toxic chemicals such as lead, which was present at 140 ppm in the lime wash. One explanation that may account for the sudden death of numerous larvae, pupae, and adults in the wood is cold winter temperatures. The warehouse was probably left unheated for at least one year before the military took over in 1846. If this is so, then dead larvae, pupae, and adults of the larder beetle must have been entombed in the wood for over a hundred years.

We can only speculate on the possible origin of the larder beetles in the warehouse. Records indicate that there was little contact between Lower Fort Garry and eastern Canada (Van der Putten, pers. comm.), but supplies were frequently received from England. It would appear then that this insect originated from England on or in any number of things listed by Hinton (1945).

Priobium sericeum (Say)

The numerous small exit holes and dustlike powder on the oak beams indicated that the beams had been attacked by an anobiid beetle. Adults obtained from rearing the larvae in the beams were not death watch beetles, *Xestobium rufovillosum*, as expected, but another member of the same family, *Priobium sericeum* (Fig. 3). Larvae and exit holes were found at the end of the beams up to 1.2 m from the wall and in the lintels. Adults of this species emerged in the laboratory on 14 February and 14 March 1977 and 5 January 1978.

This is a native species, which White (1962) recorded from dead branches of oak, wild cherry, and hickory. According to Simeone (1962), it is distributed from Nova Scotia to Wisconsin in the north, southwestward to Arizona, and southeastward to Texas and Florida. The Canadian National Collection, Ottawa, has specimens only from Nova Scotia, New Brunswick, Quebec, and Ontario. This is the first record of *Priobium sericeum* in Manitoba.

After the oak was floated down the Red River to Lower Fort Garry, it probably became infested by a local population of *Priobium sericeum*, which laid eggs in exposed wood such as knots, cracks, and crevices. After hatching the larvae entered the wood and riddled it with tunnels, packed with powdery dust. The small round surface holes mark exits of adults of *Priobium sericeum*. Populations of this insect started either outside the warehouse when the oak was stacked ready for use or within the warehouse from infested oak used in ax handles, farm implements, furniture, or frame-work of Red River carts.

Pseudohadrotoma sp.

Only four adults (Fig. 5) of this species were obtained. Dr. E.C. Becker, Biosystematic Research Institute, Ottawa, indicated that it is undescribed. Adults emerged on 2 and 14 February and 19 December 1977, and 4 June 1978. In Beal's key (1967) to species of *Pseudohadrotoma*, the new species is close to *Pseudohadrotoma falsa* (Horn), which Beal indicated as being beaten from *Quercus* and which is probably a general scavenger feeding on the remains of other insects in burrows of wood. This new species probably fed on the remains of larger beetles in the oak beams and did not cause primary damage to the wood.

Of the three species of insects reared from infested oak beams at Lower Fort Garry, Manitoba, only *Dermestes lardarius* and *Priobium sericeum* caused primary damage. Individuals of the former species, although most abundant, were all killed, apparently by extreme cold weather when the warehouse was left unheated for a year. Those of the latter species are still thriving.

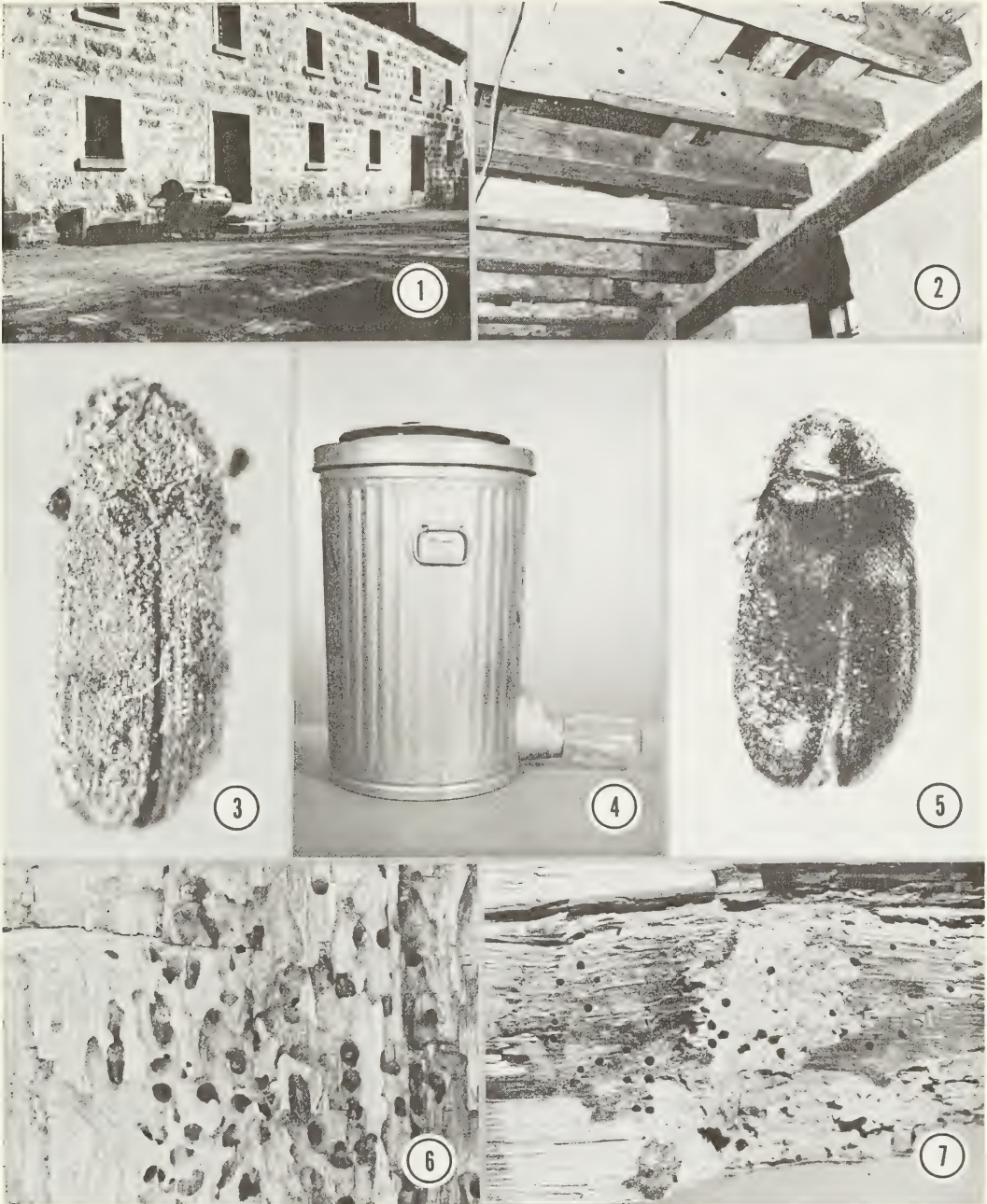
ACKNOWLEDGMENTS

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Figures 1 – 7. Fig. 1, limestone warehouse, Lower Fort Garry, Manitoba; Fig. 2, oak beams on ceiling showing whitewash and section of beam restored; Fig. 3, adult of *Priobium sericeum* just emerged from oak beam; Fig. 4, modified galvanized metal garbage can used for rearing insects in oak beams; Fig. 5, adult of *Pseudohadrotoma* sp.; Fig. 6, dead adults of *Dermestes lardarius* in oak beam; Fig. 7, holes in oak beam made by *Dermestes lardarius* and *Priobium sericeum*.

**OBSERVATIONS ON THE SNOW SCORPIONFLY *BOREUS BRUMALIS* FITCH
(BOREIDAE: MECOPTERA) IN SUDBURY, ONTARIO**

J.D. SHORTHOUSE

Department of Biology

Laurentian University

Sudbury, Ontario

P3E 2C6

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Adults of the snow scorpionfly, Boreus brumalis Fitch, are common on the surface of snow from February to March within the city limits of Sudbury, Ontario when the temperature rises above 0 C. Ease of locating a mate and dispersal are the suggested reasons for this mid-winter activity.

Les adultes du Mécoptère Boreus brumalis Fitch sont communs sur la neige dans la ville de Sudbury, Ontario, en février et en mars, quand la température s'élève au-dessus de 0 C. Le fait que la rencontre des partenaires sexuels et la dispersion soient faciles est suggéré comme cause d'une telle activité hivernale.

The occurrence of active insects on the surface of snow in mid-winter is to most biologists an extraordinary event. Snow scorpionflies of the genus *Boreus* exhibit this behavior as a regular part of their life cycle (Crampton, 1940; Byers 1954; Chapman, 1954; Webb *et al.*, 1975; Penny, 1977) and although they are not rare insects, they are seldom observed. This paper reviews the biology of *Boreus brumalis* Fitch and records the species on snow-covered hills within the city limits of Sudbury, Ontario (46°30'N, 81°00'W) in February and March of 1977 and 1978. Suggestions also are given as to why *Boreus brumalis* emerges onto the surface of the snow.

The Family Boreidae consists of two genera, *Boreus* and *Hesperoboreus* (Penny, 1977) with members of the genus *Boreus* occurring in Europe, Asia, and North America. Ten species of *Boreus* are recorded from North America with only two, *Boreus brumalis* and *Boreus nivoriundus* Fitch occurring east of the Rocky Mountains (Penny, 1977). *Boreus brumalis* is considered the most common North American species (Byers 1954). It is usually found in deciduous woodlands and has been recorded from central Ontario and Quebec south to Tennessee, with the western limits being isolated populations in Illinois, Wisconsin, and Minnesota (Webb *et al.*, 1975).

Both male and female *Boreus brumalis* are small (2.5 mm to 5.0 mm), stout, black insects with biting mouthparts on the ventrally extended rostrum, a characteristic common to the Order (Richards and Davies, 1977). The legs and antennae are long and black. Wings of the male are reduced to a pair of slender vestiges, tapering apically to an acute point (Fig. 1), with coarse black setae found along the lateral and medial margin. The hind wings are much smaller and lie in a groove in the fore-wing. The genital claspers are flexed dorsally over the abdomen giving the scorpion-like appearance. Wings of the female are further reduced to scale-like, oval lobes (Fig. 2). The functional ovipositor is elongated and consists of modified 9th to 11th abdominal segments (Cooper, 1940). For further details on the morphology of Boreidae, see Penny, 1977.

Both the immatures and adults of all species live in and feed on mosses. The eggs are laid in late fall at the base of mosses and the larvae hatch in about ten days (Webb *et al.*, 1975). Crampton (1940) reported that larvae can be found at all times of the year implying that larvae feed throughout the winter. The larvae form small chambers in compacted soil and it is thought that they aestivate throughout part of summer in these chambers (Fraser, 1943; Webb *et al.*, 1975). Descriptions of *Boreus* larvae and pupae are given by Withycombe (1922). Pupation occurs in the chambers (Fraser, 1943) and the pupal stage lasts from 4 to 8 weeks. Adults of the European species *Boreus hyemalis* (L.) emerge in

late fall and are found crawling around on mosses (Withycombe, 1922; Fraser, 1943). Adults of the North American species also emerge in the fall with Illinois populations known to crawl onto the surface of the snow from November to April (Webb *et al.*, 1975). The adults presumably continue feeding on mosses beneath the snow throughout the winter. The adults feed by thrusting their rostrum into the young shoots of mosses, chewing off the apex, then eating down into the core (Fraser, 1943).

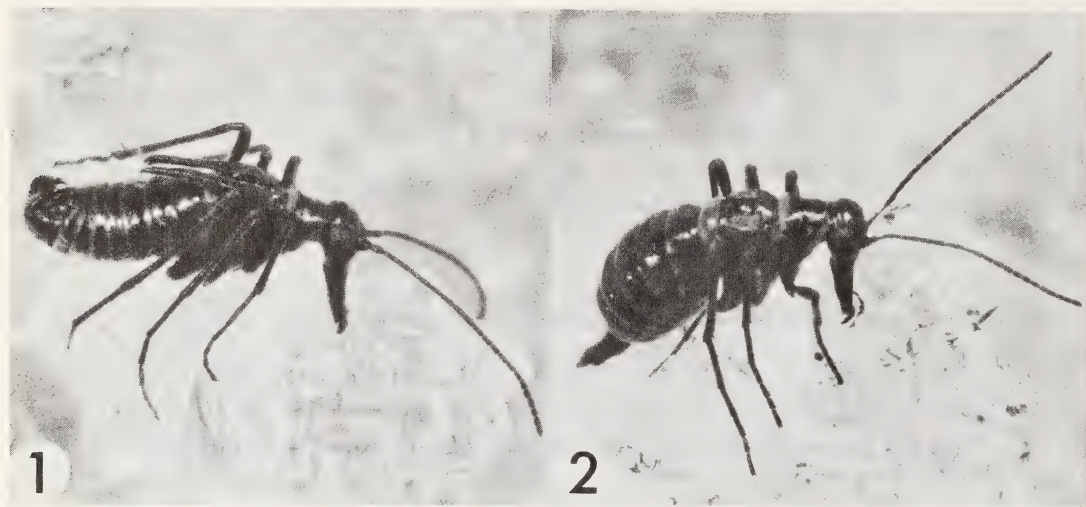


Figure 1 and 2. Fig. 1, Male *Boreus brumalis*. Fig. 2, Female *Boreus brumalis*. Magnification X 15.

The life cycle of *Boreus brumalis* in Sudbury is likely similar to that of *brumalis* in Illinois (Webb *et al.*, 1975). No adults were observed until mid-winter; however it is possible that some adults emerge in the fall and remain under the snow for several months before crawling to the surface. The first adults were found on 12 February 1977 and were common until 19 March on days with suitable temperatures. No adults were seen in 1978 before 4 March. Many copulating pairs were found indicating that oviposition also takes place in late winter.

Adults come to the surface along passage-ways found next to the stems of shrubs and trunks of trees. Apparently they only come to the surface when the air temperature approaches 0 C (Wojtusiak, 1950; Chapman, 1954), although one European species has been reported active at -5.5 C (Fjellberg and Greve, 1968). On 12 February 1977, the air temperature in Sudbury had risen to 2.3 C and on 19 March to 2.7 C, both being days that followed periods of subzero temperatures. The same occurred on 11 March 1978 when the temperature was 2.4 C. The adults were always most common and active around 1400 hours; however, they retreated beneath the snow around 1700 hours.

The sex ratio of the 107 specimens collected in Sudbury was 0.57, similar to that recorded for other species. (Fjellberg and Greve, 1968). Adults are easily spotted against the white snow and often were as common as 1 per 4m². The largest populations were found in seral white birch-red maple-red oak forests on south-facing slopes (Fig. 3). The snow depth on dates of collection was about 30 cm.



Figure 3. Typical winter habitat of *Boreus brumalis* on a hillside dominated by white birch, red maple, and red oak within the city limits of Sudbury, Ontario.

The mating behavior of *Boreus* species is peculiar and has been described for several species (Cockle, 1908; Withycombe, 1926; Cooper, 1940; Crampton, 1940). The *Boreus brumalis* male upon finding a female, springs and seizes her body with his modified wings. Once she is securely gripped, the male uses his hind legs and claspers to manoeuvre her into a position parallel to and above his body. He then releases his wings allowing the female to flex her rostrum between his coxae, fold her antennae between her legs, and stretch her legs posteroventrally. Once in this position the male then grips her fore-legs and rostrum with his wings. This position with the female above the male is maintained throughout copulation. The male usually runs about during copulation while the female remains motionless.

The ability to remain active at low temperatures and to use the snow surface as a habitat is a fascinating adaptation shared by few other arthropods. Besides *Boreus*, only a few species of Chironomidae, Heleomyzidae, Tipulidae, Trichoceridae, Plecoptera, Collembola, and spiders have been reported using the snow surface (Wojtusiak, 1950; Hågvar, 1973; Hågvar, and Ostbye, 1973). Some spiders even form webs on the surface where they trap collembolans.

Little has been written as to reasons why scorpionflies climb to the surface in mid-winter. The obvious benefit would be ease of movement since the smooth surface of snow provides an alternative terrain with few impediments to dispersal. Some individuals were observed hopping a distance of 2 m in 5 minutes, while one was found 70 m from shore on a snow covered lake, obviously far from its site of emergence. Ease of locating the opposite sex also would be enhanced in this environment while the risk of attack by predators would be reduced. Some spiders were found on the surface at the same time as the Sudbury *Boreus*, but they were not observed feeding.

The temperature of the subnivean air space remains near 0 C with about 30 cm of snow cover, regardless of the external air temperature (Coulianos and Johnels, 1962) and this is obviously sufficiently warm for scorpionflies to locate stems and tree trunks and climb to the surface. Once on the surface their dark coloration would absorb heat thus raising the body temperature higher than it would

have been under the snow. This additional heat probably contributes to their improved ability to disperse on the snow surface. How they get back under the protective snow cover when the air temperature drops and the cue for their return remain as fascinating problems.

Although members of the genus *Boreus* are excellent candidates for further studies of cold hardiness, their greatest value may come from serving educators with another intriguing example of insect adaptability. Educators and biologists alike should be on the alert for winter insects since they vividly contradict the common misunderstanding that all in the insect world is inactive from October to April.

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NOTES ABOUT CLASSIFICATION OF THE SOUTH AMERICAN PTEROSTICHINI WITH A
KEY FOR DETERMINATION OF SUBTRIBES, GENERA AND SUBGENERA
(COLEOPTERA: CARABIDAE)

S.L. STRANEO

V. Campari 8E

27100 Pavia

ITALY

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Treated in the key, which is based on characters of adults, are 37 genera and 20 subgenera, arrayed in the following seven subtribes: Morionina (two genera); Cratocerina (one genus); Microcephalina (one genus); Euchroina (four genera); Pterostichina (24 genera, 18 subgenera); Antarctiina (four genera); and Chaetogenyina (one genus, two subgenera). Excluded from the Pterostichina and ranked as tribes are the Catapiesini and Agonini.

Tratados en la llave, el cual está basado en el original de los adultos, se encuentran 37 géneros y 20 sub-géneros, compilados en los siete siguientes sub-tribus: Morionina (dos géneros); Cratocerina (un género); Microcephalina (un género); Euchriona (cuatro género); Pterostichina (24 géneros, 18 sub-géneros); Antarctiina (cuatro géneros); y Chaetogenyina (un género, dos sub-géneros). Excluidos del Pterostichini y clasificados como tribus están los Catapiesini y Agonini.

INTRODUCTION

In 1976, the late Hans Reichardt (Museu de Zoologia da Universidade de São Paulo, Brazil) suggested to me a revision at the generic level of the South American Pterostichini, which he needed for his proposed synopsis of the genera of Neotropical Carabidae. This work was published posthumously, in an incomplete state (Reichardt, 1977). Preparation of my contribution was delayed for a variety of reasons, and I did not know about plans for completion of the general synopsis, following Dr. Reichardt's sudden and untimely death. The synopsis of the South American Pterostichini was published (Straneo, 1977) in Italian. Some months ago, George E. Ball invited me to write an English translation of my key for publication in *Quaestiones Entomologicae*, as a supplement to Reichardt's work.

The key I offer here is a translation with some modifications in style, as well. I have chosen to restrict the key and preliminary classification to taxa that are either confined to South America, or whose relatives are in South America. Thus, I do not deal with the northern elements of the Neotropical fauna, except for *Dyschromus*, which is the only genus of the Euchroina known from the northern hemisphere.

Only a few references are given here. References to descriptions of taxa can be obtained from Csiki (1929 and 1930), Blackwelder (1944 and 1957) and Reichardt (1977).

Previously (Straneo, 1977), I presented a list of the generic types of genera and subgenera of South American Pterostichini. Generic types of the following taxa were fixed in that paper: *Oribazus* Chaudoir; *Meropalpus* Tschitscherine; *Pseudabarys* Chaudoir; *Cynthidia* Chaudoir; *Ogmopleura* Tschitscherine; *Trirammatus* Chaudoir; *Feroniomorpha* Tschitscherine; *Parhypates* Motschulsky; *Agraphoderes* Bates; *Eutany*s Tschitscherine; *Adrimus* Bates; *Feroniola* Tschitscherine; and *Antarctiola* Straneo. Also, the genus *Cephalostichus* was described as new.

NOTES ABOUT CLASSIFICATION

Two types of problems were encountered in study of classification of the South American Pterostichini. First is the matter of inclusion and exclusion of reasonably clearly defined groups of

genera. Second is the matter of ranking at the genus-group level.

I exclude from the Pterostichini the catapielines, based on conclusions of Reichardt (1973), though the exact position of the group remains to be determined. Presently, it is ranked as a tribe, and placed near the truncatipennian assemblage of tribes. I also exclude the agonines, which I regard as a group related to, but at the same rank as, the pterostichines, even though various recent authors (for example Lindroth 1966: 441–442; Erwin *et al.*, 1977: 4.25–4.32; and Reichardt, 1977: 406) combine these two groups in a single tribe.

I include as a subtribe of the Pterostichini the morionines because, first, many character states of adults of these two groups are shared, and second, because morionines are traditionally regarded as a subgroup of the Pterostichini, and at present carabid specialists are not unanimous about placement and ranking of morionines. Thus, it seems best to follow tradition.

Ball (in Reichardt, 1977: 408) questioned inclusion of the chaetogenyines in the Pterostichini, but for the present, I prefer to maintain the *status quo*.

Inclusion of the Cratocerina, Microcephalina (= *Tichoniina* Reichardt 1977: 407), Euchroina, and Antartchiina in the Pterostichini has not been challenged by other recent authors.

Ranking at the level of genus-group (genera and subgenera) is a problem in the Pterostichini. Many of these taxa were ranked by previous authors as subgenera of *Pterostichus* (see, for example, Csiki, 1930 and Blackwelder, 1944: 35). Provisionally, at least, I think it best to exclude *Pterostichus* (*sensu latiore*) from the southern hemisphere by removing from it all South American species. Future studies will have to be made to determine relationships of these taxa to their northern counterparts.

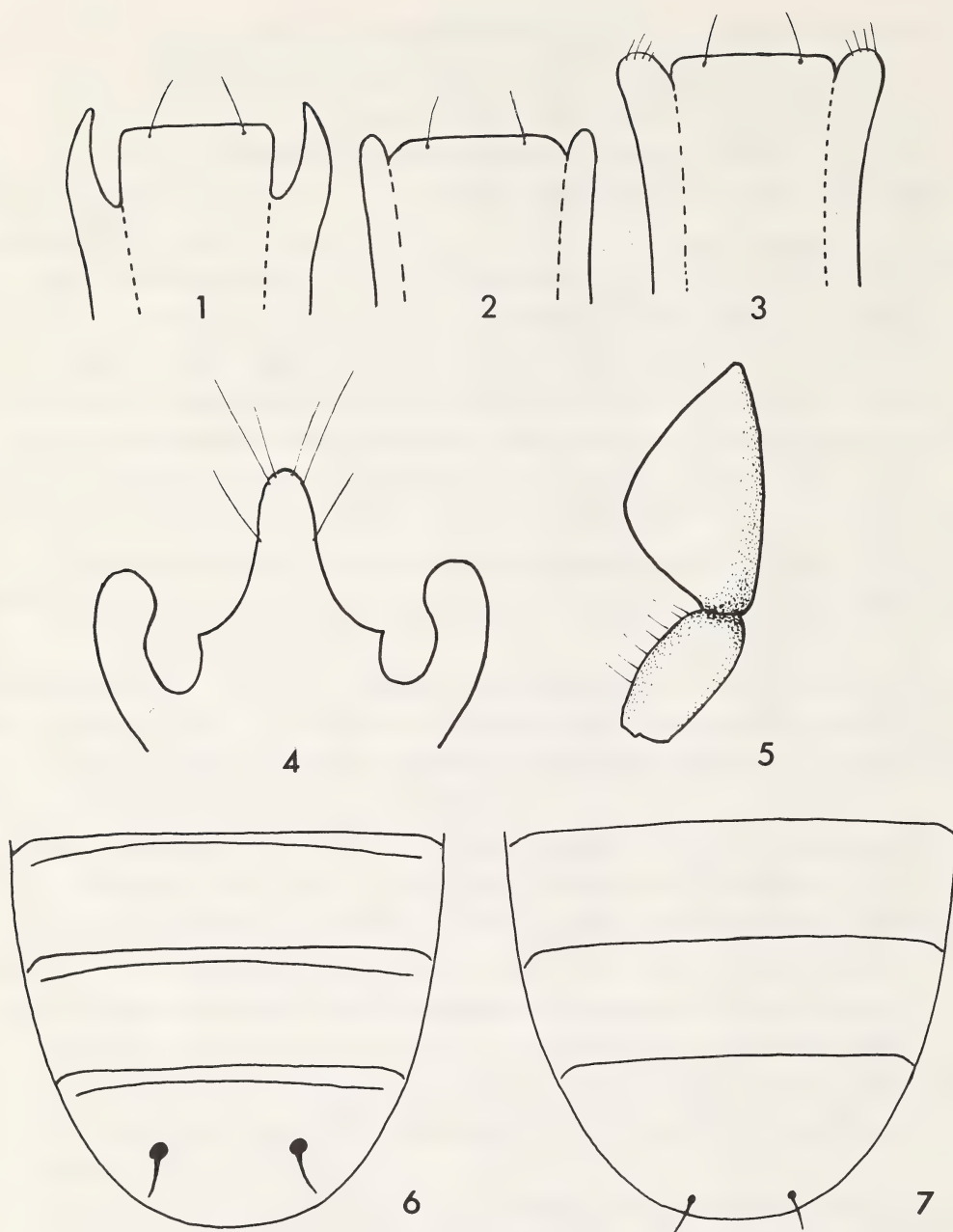
Limits of many of the South American genera are not well defined on the basis of adult character states, and I feel uncertain about the validity of some of these groups. Some groups ranked by me as subgenera will probably be treated as genera by other authors. As well, some of my genera will probably be combined by other authors. In brief, the present arrangement is unstable, and the South American pterostichine fauna is a rich field for systematic research.

In view of the circumstances outlined above, it may seem presumptuous to offer a key for determination of the higher taxa of South American Pterostichini. However, a provisional key seems better than nothing, and I hope that it will be useful both as a stepping stone to development of a better one, and above all, as a stimulus to investigate the interesting, highly diverse and divergent Neotropical pterostichine fauna.

Key to adults of subtribes and genera of the South American Pterostichini

- 1 (0) Anterior tibia markedly dilated toward apex. Antennomeres 4–10 moniliform (i.e., each article thickened, and about as wide as long) 2
- 1' Anterior tibia average, not markedly dilated apically. Antennomeres 4–10 filiform, articles not thickened, and either distinctly longer than wide (most taxa) or as long as wide 4
- 2 (1) Anterior tibia with terminal angle extended as evident tooth; position of scutellum at base of elytra normal. Body more or less “scaritoid” and pedunculate 3
 -MORIONINA
- 2' Anterior tibia with terminal angle not extended as evident tooth. Scutellum forward in relation to bases of elytra. Body convex, not pedunculate
 -CRATOCERINA, *Cratocerus* Dejean
- 3 (2) Mentum with tooth bilobed. Length of body more than 12 mm *Morion* Latreille
- 3' Mentum with tooth simple. Length of body less than 12 mm *Moriosomus* Motschulsky
- 4 (1') Labium with apex of ligula extended forward, and with long setae (Fig. 4). Other

	mouthparts and basal antennomeres with some long and stiff setaeCHAETOGENYINA, <i>Camptotoma (sensu latiore)</i> Reiche.....	5
4'	Ligula with apex not prominently prolonged forward (Fig. 1,2,3). Antennomeres and mouthparts without supernumerary long and stiff setae	6
5 (4)	Head with single pair of supraorbital setigerous punctures. Pronotum with single pair of lateral setigerous punctures, anterior pair absent	<i>Camptotoma (sensu stricto)</i>
5'	Head with two pairs of supraorbital setigerous punctures. Pronotum with two pairs of lateral setigerous punctures.....	<i>Camptotoma (Chaetogenys)</i> van Emden
6 (4')	Apex of labial paraglossa with few setae (Fig. 3).....	ANTARCTIINA
6	Apex of paraglossa without setae (Fig. 1,2).....	10
7 (6)	Penultimate labial palpomere with row of setae (more than two). Pronotum with two pairs of lateral setigerous punctures in anterior half. Anterior surface (ventral surface, in repose) of each femur with one or two rows of setigerous punctures, latter more numerous on posterior femora. Color red-brown, body very convex, short and stout, elytra only slightly longer than wide. Range - San Ambrosio Island, Chile.....	<i>Kuschelinus</i> Straneo
7'	Penultimate labial palpomere bisetose. Body more elongate, more slender, and less convex	8
8 (7')	Anterior surface of femur with row of long setae. Abdominal sterna IV-VI each with transverse row of setae.....	<i>Antarctiola</i> Straneo
8'	Anterior surface of femur with one or two setae only. Abdominal sterna IV-V each with single pair of setae, only	9
9 (8')	Penultimate tarsomere of each tarsus markedly bilobed	<i>Abropus</i> Waterhouse
9'	Penultimate tarsomere not bilobed, average for Pterostichini	<i>Metius</i> Curtis
10 (6')	Sternum VI with setigerous punctures deep and rather large, located near transverse mid-line (Fig. 6). Abdominal sterna IV-VI each distinctly and transversely bordered basally. Elytron without scutellar stria. Terminal palpomeres various	11
10'	Sternum VI with setigerous punctures normal, not foveate; OR subfoveate, but located along apical margin (Fig. 7). Scutellar stria present or absent. Terminal palpomeres subcylindrical or fusiform	PTEROSTICHINA..... 15
11 (10)	Terminal labial palpomere subcylindrical or fusiform. Elytral interval 3 with one or more discal setigerous punctures	EUCHROINA (in part), <i>Bothynoproctus</i> Tschitscherine
11'	Terminal labial palpomere more or less triangular. Elytral interval 3 without discal setigerous punctures	12
12 (11')	Penultimate labial palpomere plurisetose (Fig. 5). Terminal maxillary and labial palpomeres dilated apically, latter with width at apex subequal to length of medial margin. Body form like that of an <i>Abax</i> adult. Dorsal surface brilliantly metallic	MICROCEPHALINA, <i>Tichonilla</i> Strand
12'	Penultimate labial palpomere bisetose	EUCHROINA (in part)..... 13
13 (12')	Body length more than 20 mm. Head and prothorax blue green metallic, elytra coppery with pronounced metallic luster. Elytron with striae deeply impressed, intervals convex ...	<i>Lobobrachus</i> Sharp
13'	Body length less than 20 mm. Color and elytral sculpture various.....	14
14 (13')	Labial mentum with epilobe not extended to apex of lateral lobe; ligula moderately protruded beyond mental tooth; terminal labial palpomere of male markedly dilated and triangular, apical and lateral margins subequal; of female, less dilated, with medial and apical margins subequal. Elytron with striae deeply impressed, intervals convex	<i>Euchroa</i> Brullé



Figures 1 – 7. Fig. 1–4. Outline drawings of apical portion of prementae of various pterostichines. Fig. 1 and 2, paraglossae without apical setae; Fig. 3, paraglossae setose (Antarctiina); Fig. 4, ligula setose (Chaetogenyina). Fig. 5. Outline drawing of labial palpomeres 2 and 3 of *Microcephalina*. Fig. 6 and 7. Outline drawings of ventral aspect of abdominal sterna IV–VI. Fig. 6, sterna sulcate, margined along base, and with setigerous punctures of sternum VI mediad (*Euchroina*); Fig. 7, regular or average sterna for *Pterostichini*.

- 14' Mental epilobe extended to apex of lateral lobe; ligula more elongate, markedly projected beyond apex of mental tooth; terminal labial palpomere less dilated apically (in male, apical margin much shorter than medial margin; in female, still less dilated). Elytron with striae less deeply impressed, intervals only slightly convex. Range - mountains of central Mexico, and island of Hispaniola..... *Dyschromus* Chaudoir
- 15 (10') Antenna short, antennomeres 4–10 each slightly wider than long. Abdominal sterna IV–VI each sulcate along base, or with vestigial sulcus each side, only..... *Cephalostichus* Straneo
- 15' Antenna average, elongate, antennomeres 4–10 distinctly longer than wide. Abdominal sterna sulcate or not..... 16
- 16 (15') Sterna IV–VI each entirely transversely sulcate and margined basally..... 17
- 16' Sterna IV–VI not entirely sulcate and not bordered along basal margin, with or without short sulcus each side..... 29
- 17 (16) Elytron with only five deeply impressed striae; intervals markedly convex, catenate..... *Oribazus* Chaudoir
- 17' Elytron normally striate; intervals uninterrupted throughout length of disc 18
- 18 (17') Elytron with interval 3 impunctate 19
- 18' Elytral interval 3 with one, two, or three setigerous punctures 22
- 19 (18) Alternate intervals of elytron with irregular impressions. Pronotum with single postero-lateral impression each side..... *Apsaustodon* Tschitscherine
- 19' Intervals of elytron smooth, without irregular impressions 20
- 20 (19') Dorsal surface of elytra with blue-violaceous metallic luster. Pronotum with two postero-lateral impressions each side. Body length more than 10 mm. Setigerous punctures of abdominal sternum VI slightly larger than usual..... *Haplobothynus* Tschitscherine
- 20' Elytra with dorsal surface black, without metallic luster 21
- 21 (20') Larger, body length 14–15 mm. Body slender, slightly convex. Dorsal surface of elytra black, glossy, but not iridescent (Middle American specimens of this genus have the elytra distinctly iridescent [geb])..... *Ophryogaster* Chaudoir
- 21' Smaller, body length about 8.5 mm. Elytra markedly convex, dorsal surface slightly iridescent..... *Hybothecus* Chaudoir
- 22 (18) Tarsal claws pectinate *Abaridius* Chaudoir
- 22' Tarsal claws smooth, not pectinate 23
- 23 (22') Elytron with interval 3 impunctate *Pseudabarys* Chaudoir
- 23' Elytron with interval 3 at least bipunctate..... 24
- 24 (23') Transverse sulcus of each abdominal sternum with large and deep punctures..... *Sierrobis (sensu latiore)* Straneo 25
- 24' Transverse sulci of abdominal sterna impunctate..... 26
- 25 (24) Body slender, Apical blade of median lobe of most males asymmetric, right side more developed than left..... *Sierrobis (sensu stricto)*
- 25' Body stouter. Median lobe either symmetrical, or left side slightly more developed than right *Sierrobis (Pachyabaris)* Straneo
- 26 (24) Elytron with scutellar stria more or less developed. (Body form like that of *Poecilus cupreus*, or *Poecilus lucublandus*)..... *Pachytheus* Chaudoir
- 26' Elytron without scutellar stria 27

- 27 (26') Terminal labial palpomere of male triangular, medial margin twice length of apical margin..... *Meropalpus* Tschitscherine
- 27' Terminal labial palpomere subcylindrical or fusiform 28
- 28 (27') Abdominal sterna with setigerous punctures slightly larger and deeper than usual. Smaller (body length 9–10 mm) *Eumara* Tschitscherine
- 28' Abdominal sterna with setigerous punctures of average size. Larger, or same size as above *Marsyas* Putzeys
- 29 (16') Tarsal claws pectinate. Head wide; eyes large hemispherical. Body length 4–6 mm. Elytral interval 3 with single setigerous puncture. Abdominal sterna IV–VI without transverse sulci laterally *Abaris* Dejean
- 29' Tarsal claws smooth, not pectinate. Length more than 6 mm; or eyes small to average in size 30
- 30 (29') Sterna IV–VI each with transverse sulcus widely interrupted medially (complete in few specimens of *Blennidus fontainei* Tschitscherine) 31
- 30' Sterna IV–VI without partial transverse sulcus and border; with or without irregular longitudinal impressions laterally 34
- 31 (30) Labrum metallic *Cynthidia* Chaudoir
- 31' Labrum not metallic 32
- 32 (31') Partial sulci of sterna IV–VI each with row of rather wide and deep punctures. Metepisternum of thorax short or moderately elongate *Ogmopleura* Tschitscherine
- 32' Partial sulci of sterna IV–VI smooth, without row of wide and deep punctures. Metepisternum elongate, with lateral side 1.5 times longer than anterior width *Blennidus (sensu latiore)* Motschulsky 33
- 33 (32') Dorsal surface of body coppery, shiny (similar to *Poecilus cupreus*; rather flattened *Blennidus (Pseudocynthidia)* Straneo
- 33' Dorsal surface of body black; more convex *Blennidus (sensu stricto)*
- 34 (30') Elytral interval 3 impunctate *Feroniola* Tschitscherine
- 34' Elytral interval 3 with at least one setigerous puncture 35
- 35 (34') Elytral intervals 5 and 7 with some setigerous punctures *Metoncidus* Bates
- 35' Elytral intervals 5 and 7 impunctate 36
- 36 (35') Elytral interval 3 with two or more setigerous punctures 37
- 36' Elytral interval 3 with single setigerous puncture 46
- 37 (36) Intercoxal process of prosternum with two setigerous punctures near apex *Parhypates (Argutoridius)* Chaudoir
- 37' Intercoxal process glabrous, without setigerous punctures 38
- 38 (37') Metepisternum short, anterior and lateral margins subequal *Parhypates (sensu latiore)* Motschulsky 39
- 38' Metepisternum elongate, lateral margin longer than width at anterior margin *Trirammatus (sensu latiore)* Chaudoir 43
- 39 (38) Small, body length 7–9 mm. Form stout. Pronotum convex, only slightly narrowed basally. Range - high altitudes in Andes of Ecuador *Parhypates (Agraphoderes)* Bates
- 39' Size generally larger. Form slender. Pronotum only slightly convex, or slightly flattened, generally evidently narrowed toward base 40
- 40 (39') Head with two pairs of supraorbital setigerous punctures 41
- 40' Head with one or three pairs of supraorbital setigerous punctures 42
- 41 (40) Lateral margins of lateral lobes of mentum smooth, not crenulate. Frons with

- impressions. Elytron with basal ridge complete. At least hind tarsomere 1 sulcate laterally. Mandibles shorter *Parhypates (sensu stricto)*
- 41' Mentum with lateral margins of lateral lobes crenulate. Frontal impressions indistinct or nearly so. Elytron with basal ridge complete or rudimentary. Mandibles longer *Parhypates (Eutanys)* Tschitscherine
- 42 (40') Head with single pair of supraorbital setigerous punctures *Parhypates (Antarctobium)* Tschitscherine
- 42' Head with at least three pairs of supraorbital setigerous punctures *Parhypates (Chaetuchenium)* Tschitscherine
- 43 (38') Elytron without scutellar stria *Trirammatus (sensu stricto)*
- 43' Elytron with scutellar stria 44
- 44 (43') Mentum with tooth bilobed. Pronotum with complete anterior submarginal sulcus *Trirammatus (Meraulax)* Tschitscherine
- 45 (44') Prosternum with intercoxal process smooth, not margined apically. Pronotum not obliquely depressed near postero-lateral angles *Trirammatus (Feroniomorpha)* Tschitscherine
- 45' Intercoastal process of prosternum with apex margined. Pronotum obliquely depressed near postero-lateral angles *Trirammatus (Plagioplatys)* Tschitscherine
- 46 (36') Metepimeron with posterior margin obliquely truncate. Metepisternum with lateral margin only slightly longer than width at anterior margin. Posterior tarsomeres longitudinally deeply sulcate on outer and inner sides; anterior tarsomeres of male slightly dilated obliquely, ventral adhesive vestiture confined to inner (medial) half of tarsomeres 1–3. Pronotum with anterior marginal sulcus complete and deep *Adrimus* Bates
- 46' Metepimeron regular in form, posterior margin rounded 47
- 47 (46') Metepisternum short, width at base and length of lateral margin subequal. Anterior tarsomeres of male normally, symmetrically dilated *Parhypates (Paranortes)*
- 47' Metepisternum elongate (specimens of most taxa), or short. Male with anterior tarsomeres obliquely dilated 48
- 48 (47') Pronotum with more than two pairs of lateral setigerous punctures; not pedunculate *Oxycrepis (sensu stricto)* Reiche
- 48' Pronotum with one or two pairs of lateral setigerous punctures; pedunculate or not 49
- 49 (48') Pronotum not pedunculate *Loxandrus* LeConte
- 49' Pronotum pedunculate 50
- 50 (49') Pronotum as wide as long; lateral margin evidently angulate at level of anterior setigerous puncture. Elytral striae shallow, very slightly punctulate; intervals flat, interval 3 with series of nine setigerous punctures near stria 2 *Oxycrepis (Prostolonis)* Mateu
- 50' Pronotum more narrowed anteriorly, wider than long; lateral margin rounded or only slightly angulate at level of anterior setigerous puncture. Elytral striae deeper and markedly punctulate; intervals more or less convex, interval 3 with single setigerous puncture *Oxycrepis (Stolonis)* Motschulsky

CHECKLIST OF SOUTH AMERICAN PTEROSTICHINI: SUBTRIBES, GENERA, AND SUBGENERA

Subtribe MORIONINA

1. *Morion* Latreille, 1810
2. *Moriosomus* Motschulsky, 1864

Subtribe CRATOCERINA

3. *Cratocerus* Dejean, 1829

Subtribe MICROCEPHALINA

4. *Tichonilla* Strand, 1942

Subtribe EUCHROINA

5. *Lobobrachus* Sharp, 1885
6. *Euchroa* Brullé, 1834
(*Dyschromus* Chaudoir, 1835)
7. *Bothynoproctus* Tschitscherine, 1900

Subtribe PTEROSTICHINA

8. *Oribazus* Chaudoir, 1874
9. *Apsaustodon* Tschitscherine, 1901
10. *Haplobothynus* Tschitscherine, 1901
11. *Ophryogaster* Chaudoir, 1878
12. *Hybothecus* Chaudoir, 1874
13. *Sierrobisus* (*sensu latiore*) Straneo, 1951
 - 13.1 *Sierrobisus* (*sensu stricto*)
 - 13.2 *Pachyabaris* Straneo, 1951
14. *Pachythecus* Chaudoir, 1874
15. *Meropalpus* Tschitscherine, 1900
16. *Marsyas* Putzeys, 1846
17. *Eumara* Tschitscherine, 1901
18. *Pseudabarys* Chaudoir 1873
19. *Abaridius* Chaudoir 1873
20. *Abaris* Dejean, 1831
21. *Cynthidia* Chaudoir, 1873

- 22. *Blennidus (sensu latiore)* Motschulsky, 1865
 - 22.1 *Blennidus (sensu stricto)*
 - 22.2 *Pseudocynthidia* Straneo, 1953
- 23. *Ogmopleura* Tschitscherine, 1898
- 24. *Trirammatus (sensu latiore)* Chaudoir, 1838
 - 24.1 *Trirammatus (sensu stricto)*
 - 24.2 *Plagioplatys* Tschitscherine, 1900
 - 24.3 *Meraulax* Tschitscherine, 1900
 - 24.4 *Feroniomorpha* Solier, 1849
- 25. *Parhypates (sensu latiore)* Motschulsky 1865
 - 25.1 *Parhypates (sensu stricto)*
 - 25.2 *Agraphoderes* Bates, 1891
 - 25.3 *Eutanys* Tschitscherine, 1900
 - 25.4 *Anarctobium* Tschitscherine, 1900
 - 25.5 *Chaetauchenium* Tschitscherine, 1900
 - 25.6 *Paranortes* Tschitscherine, 1900
 - 25.7 *Argutoridius* Chaudoir, 1876
- 26. *Loxandrus* LeConte, 1852
- 27. *Oxycrepis (sensu latiore)* Reiche, 1843
 - 27.1 *Oxycrepis (sensu stricto)*
 - 27.2 *Prostolonis* Mateu, 1976
 - 27.3 *Stolonis* Motschulsky, 1865
- 28. *Adrimus* Bates, 1872
- 29. *Metoncidus* Bates, 1870
- 30. *Feroniola* Tschitscherine, 1900
- 31. *Cephalostichus* Straneo, 1977

Subtribe ANARCTIINA

- 32. *Kuschelinus* Straneo, 1963
- 33. *Metius* Curtis 1839
- 34. *Abropus* Waterhouse, 1842
- 35. *Antarctiola* Straneo 1951

Subtribe CHAETOGENYINA

- 36. *Camptotoma (sensu latiore)* Reiche, 1843
 - 36.1 *Camptotoma (sensu stricto)*
 - 36.2 *Chaetogenys* van Emden, 1958

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FOOD OF BLACK FLY LARVAE (DIPTERA: SIMULIIDAE): SEASONAL CHANGES IN GUT CONTENTS AND SUSPENDED MATERIAL AT SEVERAL SITES IN A SINGLE WATERSHED¹

DANIEL C. KURTAK²

Department of Entomology

Cornell University

Ithaca, New York 14853

U.S.A.

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Gut contents of black fly larvae and suspended material in water flowing over them in their stream habitats were studied for three years at five sites in a watershed near Ithaca, New York, U.S.A.

Suspended material was removed from water samples with a centrifuge. Total dry weight varied from 1-13 mg/l. Organic content (determined by dichromate oxidation) of suspended material varied from 8-24% of the dry weight. A portion of suspended material was analyzed microscopically. Particles were classified as diatoms and other algae, mineral fragments (silt), plant fragments, or fine material (<5 µm).

Quantity and quality of suspended material varied greatly at different sites in the watershed and with season. Headwater streams, especially in forested areas, contained larger amounts of plant fragments. In lower reaches there was more total suspended material and a larger proportion of diatoms. When stream discharges were low and steady, and sunshine was abundant, more diatoms were produced, while spring floods added more silt.

Gut contents of larvae were also analyzed microscopically, and the proportions of their constituents were found to agree generally with the proportions in the water. This indicated indiscriminate feeding. Also there was evidence that habitat preference had an influence on larval food. Diatoms often made up as much as 50% of some gut contents and were shown to be digested.

Le contenu du tube digestif de larves de mouche noire et le matériel en suspension dans l'eau recueillie autour des larves dans leurs habitats d'eau courante ont été étudiés pendant trois ans à cinq emplacements situés dans une zone de partage des eaux près d'Ithaca, dans l'état de New York (Etats-Unis).

Le matériel en suspension a été extrait des échantillons d'eau par centrifugation. Le poids sec total varie de 1 à 13 mg/l. La fraction organique (déterminée par oxydation au dichromate) du matériel en suspension constitue de 8 à 24% du poids sec. Une partie du matériel en suspension a été analysée au microscope. Les particules ont été classifiées soit comme diatomées et autres algues, fragments minéraux (argile), fragments végétaux, ou comme matériaux fins (<5 µm).

La quantité et la qualité du matériel en suspension varient beaucoup suivant les différents emplacements dans la zone de partage des eaux et suivant les saisons. Les ruisseaux de tête de cours, particulièrement dans les zones forestières, contiennent de grandes quantités de fragments végétaux. Dans les zones basses du bassin hydrographique, le matériel en suspension est plus abondant et la proportion de diatomées, plus élevée. Dans les cours d'eau abondamment ensoleillés et à écoulement lent et régulier, les diatomées sont produites en plus grands nombres, tandis les inondations printanières causent un apport accru d'argile.

Le contenu du tube digestif des larves a également été analysé au microscope. Les proportions des constituants présents sont généralement semblables à celles trouvées dans l'eau, indiquant que les larves s'alimentent au hasard. Il semble aussi que le choix de l'habitat ait une influence sur la nourriture des larves. Souvent, les diatomées constituent jusqu'à 50% du contenu de certains tubes digestifs et l'analyse montre qu'elles sont digérées.

¹Part of a thesis accepted by the Graduate Faculty of Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

²Present address: Rt. 2 Box 74R, Bishop, California 93514 U.S.A.

INTRODUCTION

Black fly larvae are filter feeders in practically all types of lotic waters, ranging from tiny streamlets to large rivers. Larvae of some species can filter material down to colloidal size (Wotton, 1976), whereas others "graze" on filamentous algae (Burton, 1973). On the basis of gut analyses, larvae feed rather indiscriminately on particulate material as shown by the studies of Anderson and Dicke (1960), Carlsson *et al.*, (1977), Chance (1970), Davies and Syme (1958), Emery (1913), Naumann (1925), Pacaud (1942), Puri (1925), Williams (1961), and Wotton (1977).

This study was designed to measure seasonal changes in the quantity and quality of suspended material at various points along the length of a stream in Tompkins County, New York, U.S.A. The gut contents of black fly larvae at each site were also examined to determine the degree of selectivity and extent to which habitat specificity influenced type of food material ingested.

MATERIALS AND METHODS

The study area

Pinkovsky (1970) and Naumann (1965) give a good ecological background for the area in central New York State (U.S.A.) where the work was done. Situated at the northern edge of the Appalachian Plateau, the area is characterized by rolling hills to the south and plains to the north. Natural vegetation is beech-maple woodland. Such vegetation exists in the more rugged areas, and on poorer soils. About 40% of Tompkins County is cultivated.

Variations in topography and vegetation produce a wide variety of stream habitats. Temperature, flow regime, discharge, substrate, and type of watershed all vary widely.

The climate is continental humid and there are large seasonal variations in stream temperature and flow. In summer months small streams dry up and large streams have low, steady, base flows. Occasionally a thunderstorm produces a freshet. In fall, winter, and spring, streams have higher and less regular flows. Snowmelt produces spring floods, with peak discharges 20–40 times the base flow (United States Geological Survey, Water Resources Data, 1965). Maximum daily water temperatures vary throughout the year and from 0 C to over 26 C for an unshaded, slow-moving stream in summer. Ice may be present for 2–3 months. Intradial variations in temperature may be high in the summer, exceeding 10 C. There are more than 20 species of black flies present in the county (Pinkovsky, 1970, p. 156).

The sites were located along Sixmile Creek and its tributaries in Tompkins County, New York. This stream is 33 km long and originates in the uplands east of Ithaca, New York at an elevation of 520 m (Fig. 1). Flowing first for approximately 5 km through mixed wood and farm land, it then passes through a gorge and over a waterfall before travelling through 7 km of farm land and a second gorge. From there it traverses a series of waterfalls, dams and reservoirs before emptying into Cayuga Lake (elevation 117 m) at Ithaca.

Sampling sites and times

The stream was sampled at Sites 1–4 (Fig. 1), chosen as representatives of different aspects of the stream (e.g. headwaters and lower reaches) and as known locations of black fly larvae. Site 1 is on one of the headwaters of Sixmile Creek where the stream is less than 1 m wide, temporary, and running through an open marshy meadow. Site 2 (Hurd Road Stream) is a small stream in a forested area, typical of many small branches of Sixmile Creek. This particular branch enters a swamp which feeds

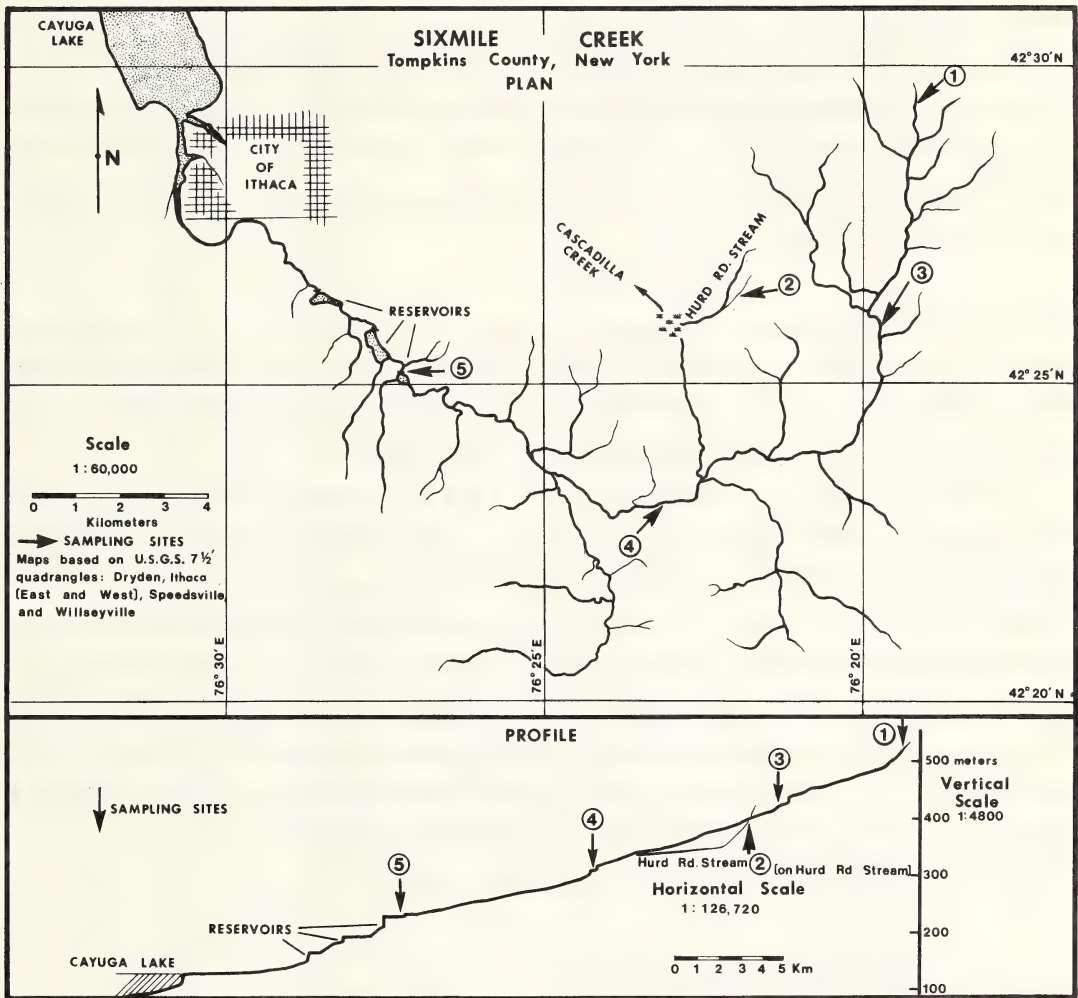


Figure 1. Sixmile Creek, Tompkins County, New York, USA. (Plan above and profile below) showing collecting sites: 1 = Sixmile Creek Headwaters (open headwater stream), 2 = Hurd Road Stream (forested headwater stream), 3 = Sixmile Creek at Sixhundred Road (forested lower reach), 4 = Sixmile Creek at Brooktondale (open lower reach), 5 = Sixmile Creek at Burns Road (dam spillway).

both Sixmile Creek and Cascadilla Creek. At Site 3, Sixmile Creek (at Sixhundred Road) has become large and permanent and flows in a rocky gorge through hilly, forested land. At Site 4 (at Brooktondale), the stream is in a shallow gorge, surrounded by farm land. Between Sites 3 and 4, there are long reaches of stream with fine-textured substrates (sand and fine gravel) which support a few larvae. A few samples were also taken at Site 5 (at Burns Road) where the stream passes over a dam spillway before entering a long gorge with forested sides. Detailed descriptions of these collection sites are given in Kurtak (1973).

Sites were visited monthly, or at least once in each of the four seasons in 1970 and 1971, and some again in 1972. Samples were taken during the daylight hours, but not at specific times.

Samples from different parts of the watershed were usually taken within a few days of each other, but not commonly on the same day, due to lack of time. If rainfall occurred in the interval between samples, a significant change in suspended material was possible.

In one instance, a special effort was made to sample the sites in a rapid sequence. Sites 1, 3, 4 and 5 were visited within a few hours.

Sampling procedure

Environmental parameters were measured at each site. These included surface velocity (measured by timing a float passing along a calibrated cord held in the current); temperature (measured to the nearest degree centigrade with an alcohol thermometer); and pH (measured with a Helige comparator using bromophenol red indicator). Notes were taken on the dimensions of the streams, the nature of the substrate, bank vegetation, and any other factors that seemed relevant.

Characteristics of the sites are summarized in Table 1 and 2. Two significant trends down the stream were increases in velocity and water temperature (in summer). Also, pH increased downstream in general, but decreased again at Site 5. Site 4 was densely populated in summer with up to 50 larvae/cm² of *Simulium pictipes*. Note that Sites 1 and 2 were both dry in the summer and early fall.

Black fly larvae were collected and returned to the laboratory alive for identification and dissection. They were identified according to Peterson (1970), Pinkovsky (1970), Stone (1964), and Stone and Jamnback (1955). Voucher specimens have been deposited in the Cornell University Insect Collection, Ithaca, New York (Lot. No. 1038). Whenever possible, identifications were made before removing the gut; otherwise, specimens were determined on the basis of preserved head capsules and skins. At least three individuals of each major species found at each site were selected and their guts removed and smeared on individual slides in Hoyer's medium. The composition of the gut content was determined in the same way as composition of samples of suspended material (see below).

The majority of the larvae collected were of the following species:

- Cnephia mutata* (Malloch)
- Prosimulium fontanum* Syme and Davies
- Prosimulium fuscum* Syme and Davies
- Prosimulium magnum* Dyar and Shannon
- Simulium decorum* Walker
- Simulium parnassum* Malloch
- Simulium pictipes* Hagen
- Simulium tuberosum* (Lunström)
- Simulium venustum* Say
- Simulium verecundum* Stone and Jamnback (species complex)
- Simulium vittatum* Zetterstedt

Table 1. Characteristics of stream sites. All sites are in Tompkins County, New York, USA.

Stream Site	Elevation (m)	Depth (m) ¹		Width (m) ¹		Velocity (m/sec) ²		Average pH	Temperature °C (seasonal range)
		Low Flow	High Flow	Low Flow	High Flow	Low Flow	High Flow		
No. 1 (Sixmile Creek headwaters)	520	dry	0.15	dry	0.5	dry	1.0	6.8	3 – 14
No. 2 (Hurd Road stream)	365	dry	0.10	dry	1.7	dry	1.0	7.2	0 – 16
No. 3 (Sixmile Creek at Sixhundred Road)	395	0.04	0.15	5.0	7.0	0.7	1.8	7.2	0 – 18
No. 4 (Sixmile Creek at Brooktondale)	290	0.05	0.60	10.0	12.0	0.9	1.2	7.6	0 – 24
No. 5 (Sixmile Creek at Burns Road)	215	0.02	0.40	15.0	15.0	0.6	1.8	7.8	0 – 26

¹ Average dimensions through a 10-m reach.² Surface velocity.

Seven liters of water were collected at each site for analysis of suspended material. The sample was dipped out as close as possible to the attachment sites of larvae when present, taking care not to stir up the substrate. Samples were stored at 4 C and usually processed within two days. They were centrifuged in a Foerst® continuous centrifuge, permitting removal of 98% of the plankton-sized material and 25–50% of the bacteria (Welch, 1948). The centrifugate was subsampled by scraping the wall of the centrifuge bowl in several vertical bands with a 4 mm wide blade. Each subsample (two per water sample) was then spread thinly on a slide in a drop of Hoyer's medium. These slides were observed at a magnification of 300 diameters using a phase contrast microscope. At least five fields laid out in an "X" pattern were observed on each slide. Areas where particles were not in a single layer were avoided. Within each field, a 50 μm x 300 μm strip was divided into 12.5 μm x 12.5 μm squares using an ocular grid. Each of these units was examined and the category of particle which filled or dominated (>50%) it was determined.

Table 2. Additional characteristics of stream sites.

Site	Type of Terrain	Substrate	Permanence	Main black fly species present
No. 1	marshy meadow	stones, trailing grass	dry July-Oct.	<i>Cnephia mutata</i> , <i>Prosimulium fontanum</i> , <i>Simulium decorum</i> , <i>S. verecundum</i>
No. 2	wooded	0.1–0.3 m stones	dry Aug.-Oct.	<i>Prosimulium magnum</i>
No. 3	wooded	horizontal shale	permanent	<i>Prosimulium fuscum</i> , <i>Simulium parnassum</i> , <i>S. tuberosum</i> , <i>S. verecundum</i>
No. 4	wooded and cropland	horizontal shale	permanent	<i>Simulium pictipes</i>
No. 5	wooded and cropland	dam spillway	permanent	<i>Simulium vittatum</i>

Particles were classified as (1) mineral fragments (identifiable by their sharp-fractured edges and including fine sand, very fine sand, and silt³, (2) organic fragments (mainly pieces of plant tissue), (3) diatoms and other algae, and (4) "fine material" less than 5 μm in diameter whose nature was undeterminable (including particles the size of fine silt and clay³). Polarized light was sometimes used to identify mineral grains by their crystalline nature. Other categories, such as filamentous algae, were employed as needed. No effort was made to count fungi, bacteria, or colloid particles. The size range of the particles was not determined in detail.

In the examination process, empty squares were not counted. Areas of large irregular particles were estimated as though the particles were smoothed to rectilinear shapes. Groups of particles less than 12.5 μm in length were assumed to be crowded together so that the space between them was negligible. Then the area (number of squares) occupied by the group was estimated. Finally, the percentage of each category in relation to the total number of squares counted was calculated for the five fields, and the mean of the two subsamples was determined. This permitted estimates of the composition of the samples on basis of area occupied by various types of particles in a thin smear.

³See United States Department of Agriculture (1951) for definitions of the sizes of soil particles.

The remaining 95% of the centrifugate was transferred to an aluminum weighing dish and dried at 60 C for 24 hours. The residue was then weighed to the nearest 0.01 mg to determine mg/l total suspended material.

Selected samples were also analyzed for oxidizable organic matter by the micro method of Maciolek (1962).

Digestion of diatoms

Although this study did not concern itself with what portion of the ingested suspended material was actually digested, a simple experiment was conducted with diatoms. Fresh, living diatoms (*Cymbella* sp.) were fed larvae of *Simulium jenningsi*, *Simulium pictipes* and *Simulium tuberosum* in the laboratory. The larvae were given no additional food, so the diatoms were retained for several hours. Every five minutes for the first 30 minutes after ingestion and at one-hour intervals for several hours thereafter, a sample of the larvae was taken. The guts were immediately removed and squashed on a slide and observed by phase contrast microscopy.

RESULTS

Suspended material and gut contents

The data from the stream water samples and gut-content analyses are presented in Tables 3 – 7. In these tables, each value for “water” represents the mean for 1–10 samples taken at that site in that month during the three years of the study. Each “gut content” value represents a mean for at least three larvae of each of the main species present when the water was sampled. The data for different species were combined if there were no significant differences among them. Coefficients of variation for groups of subsamples of a given water sample and groups of larvae collected at the same time were 10–20%. The stream stage (percent of the highest level of flow observed) and water temperature are also shown in the tables.

The dry weights of suspended material normally ranged from 1–13 mg/l ($x = 4.6$ mg/l). During flash flood periods, however, large amounts of silt and coarser mineral particles briefly raised the weights to several hundred mg/l. Such samples are not included in the means.

Usually at least 50% of the suspended material was mineral fragments or material less than 5 μ m in diameter. This largely inorganic portion (see “Organic Content” below) accounted for most of the increase in total suspended material during high water periods (e.g. during March at Site 4, Table 6). The organic portion consisted largely of plant fragments and diatoms. *Fragilaria*, *Meridion*, *Gomphonema*, and *Cymbella* were the main diatom genera seen. Visible diatom coverings on the rocks in the streams tended to be more common in the late spring and early fall than in summer or winter.

In addition to the types of materials indicated in the tables, other materials were found occasionally in the gut contents. These included fragments of filamentous algae, aquatic mites, and fragments from other arthropods, including black fly larvae. Pollen, probably of *Pinus strobus* L., was important at Site 2 on one occasion, in both guts and water.

In terms of size, mineral particles generally ranged from 5–50 μ m, diatoms from 20–100 μ m, and organic particles varied from five to several hundred μ m in diameter. Particles larger than 300–400 μ m were rarely seen in the guts. Particles less than 5 μ m, not separated as to type, often made up a large portion of the samples.

Proportions of various components of suspended material varied greatly with time and place. Water in upper reaches (Sites 1–3) contained fewer diatoms than that from lower reaches (Site 4). This trend is also clear from samples taken on one day (Table 7). The forested headwater stream at Site 2 contained

Table 3. Suspended material in water compared with the gut contents of black fly larvae at Site 1 (Sixmile Creek headwaters – open headwaters stream), 1970 – 1972. Predominant species: *Cnephia mutata*, *Prosimulium fontanum*, *Simulium decorum*, and *Simulium verecundum*.

Month	Water Temperature °C	Stream Stage (% of highest flow observed)	Total Suspended Material (dry wt. in mg/l)	Contents of Suspended Material and Gut contents (estimated microscopically)					
				Sample	Diatoms	Mineral Fragments	Organic Fragments	Particles < 5 µm	Others
January (n=1)	3 C	33%	1.7	Water	18%	18%	42%	22%	0%
February	3 C	NO DATA	NO DATA	Gut contents (<i>C. mutata</i>)	64%	6%	14%	16%	0%
				Gut contents (<i>P. fontanum</i>)	8%	23%	12%	57%	0%
				NO DATA					
March (n=1)	3 C	53%	5.6	Water	5%	16%	23%	56%	0%
April (n=2)	9 C	100%	1.8	Gut contents (all species)	23%	10%	4%	63%	0%
				Water	17%	31%	20%	32%	0%
May (n=1)	NO DATA	NO DATA	1.8	Gut contents (all species)	22%	18%	6%	54%	0%
				Water	21%	18%	27%	54%	0%
June (n=3)	14 C	40%	1.8	Gut contents (all species)	14%	12%	6%	68%	0%
				Water	21%	16%	9%	54%	0%
July-Oct.				Gut contents (all species)	27%	14%	4%	55%	0%
				STREAM DRY					
Nov.-Dec.				NO DATA					

n= Number of times visited

Table 4. Suspended material in water compared with the gut contents of black fly larvae at Site 2 (Hurd Road stream – forested headwaters stream), 1970–1972. Predominant species: *Prosimulium magnum*.

Month	Water Temperature °C	Stream Stage (% of highest flow observed)	Total Suspended Material (dry wt. in mg/l)	Contents of Suspended Material and Gut Contents (estimated microscopically)					
				Sample	Diatoms	Mineral Fragments	Organic Fragments	Particles ≤5 µm	Others
January (n=2)	0 C	68%	3.0	Water	18%	22%	9%	51%	0%
				Gut contents	14%	25%	26%	35%	0%
Feb.-March				NO DATA					
April (n=2)	4 C	100%	8.0	Water	0%	7%	10%	83%	0%
				Gut contents	6%	18%	23%	53%	0%
May (n=2)	10 C	82%	2.4	Water	2%	9%	7%	82%	0%
				Gut contents	5%	22%	18%	55%	0%
June (n=1)	11 C	9%	NO DATA	Water	NO DATA				
				Gut contents	0%	16%	19%	65%	0%
July-Oct.				STREAM DRY					
November (n=1)	9 C	91%	2.0	Water	3%	15%	61% ¹	21%	0%
				Gut contents	25%	19%	13% ¹	43%	0%
December (n=1)	4%	82%	4.0	Water	0%	25%	28%	47%	0%
				Gut contents	NO LARVAE PRESENT				

n= Number of times visited

¹Large fragments of leaves

Table 5. Suspended material in water compared with the gut contents of black fly larvae at Site 3 (Sixhundred Road - forested lower reach), 1970-1972. Predominant species: *Prosimulium fuscum*, *Simulium parnassum*, *Simulium tuberosum* and *Simulium vecundum*.

Month	Water Temperature °C	Stream Stage (% of highest flow observed)	Total Suspended Material (dry wt. in mg/l)	Contents of Suspended Material and Gut Contents (estimated microscopically)					
				Sample	Diatoms	Mineral Fragments	Organic Fragments	Particles < 5µm	Others
January (n=1)	1 C	frozen	4.7	Water	5%	26%	15%	54%	0%
				Gut contents (all species)	-----	NO LARVAE PRESENT	-----	-----	-----
February				NO DATA	-----	-----	-----	-----	-----
March (n=1)	0 C	100%	7.1	Water	0%	10%	41%	40%	0%
				Gut contents (all species)	18%	18%	11%	53%	0%
April (n=3)	8 C	80%	1.9	Water	17%	16%	23%	44%	0%
				Gut contents (all species)	11%	9%	18%	53%	0%
May (n=1)	15 C	47%	13.3	Water	1%	6%	10%	83%	0%
				Gut contents (all species)	7%	15%	21%	57%	0%
June (n=5)	15 C	33%	5.5	water	6%	23%	17%	64%	0%
				Gut contents (all species)	4%	16%	13%	67%	0%
July (n=1)	18 C	NO DATA	NO DATA	Water	-----	-----	NO DATA	-----	-----
				Gut contents (all species)	21%	17%	18%	44%	0%
August				NO DATA	-----	-----	-----	-----	-----
September (n=2)	11 C	20%	2.0	Water	5%	25%	21%	48%	1% ¹
				Gut contents (all species)	13%	21%	10%	44%	2% ¹
October				NO DATA	-----	-----	-----	-----	-----
November (n=1)	2 C	7%	1.0	Water	0%	40%	32%	28%	0%
				Gut contents (all species)	-----	NO LARVAE PRESENT	-----	-----	-----
December				NO DATA	-----	-----	-----	-----	-----

n= Number of times visited
1 Pollen

Table 6. Suspended material in water compared with the gut contents of black fly larvae at Site 4 (Brooktondale – open lower reach), 1970–1972. Predominant species: *Simulium pictipes*.

Month	Water Temperature °C	Stream Stage (% of highest flow observed)	Total Suspended Material (dry wt. in mg/l)	Contents of Suspended Material and Gut Contents (estimated microscopically)				
				Sample	Diatoms	Mineral Fragments	Organic Fragments	Particles ≤5 μm
January (n=3)	1 C	48%	4.0	Water	1%	12%	7%	80%
February (n=1)	0 C	NO DATA	5.4	Gut contents	5%	17%	10%	68%
March (n=3)	0 C	53%	12.9	Water	0%	10%	4%	86%
April (n=4)	9 C	67%	3.5	Gut contents	NO LARVAE PRESENT			
May (n=3)	13 C	68%	2.0	Water	1%	16%	10%	63%
June (n=5)	16 C	31%	8.0	Gut contents	2%	17%	4%	77%
July (n=10)	17 C	24%	3.3	Water	32%	16%	9%	43%
August (n=2)	15 C	20%	4.2	Gut contents	48%	14%	4%	34%
September (n=7)	16 C	38%	4.1	Water	12%	10%	7%	61%
October (n=6)	15 C	13%	1.4	Gut contents	16%	14%	8%	62%
November (n=3)	7 C	37%	12.6	Water	56%	18%	9%	17%
December (n=1)	4 C	93%	7.0	Gut contents	54%	6%	14%	26%
				Water	20%	25%	8%	47%
				Gut contents	30%	22%	8%	40%
				Water	39%	19%	8%	34%
				Gut contents	36%	16%	7%	41%
				Water	36%	16%	2%	46%
				Gut contents	30%	12%	11%	47%
				Water	30%	17%	6%	47%
				Gut contents	NO LARVAE PRESENT			

n= Number of times visited

Table 7. Suspended material in water compared with the gut contents of black fly larvae along the length of Sixmile Creek on June 7, 1971. Predominant species as indicated.

Site	Total Suspended Material (dry wt. in mg/l)	Water Temperature °C	pH	Estimated Discharge (m ³ /sec)	Composition of Suspended Material and Gut Contents (estimated microscopically)				
					Sample	Diatoms	Mineral Fragments	Organic Fragments	Particles <5 μm
No. 1 (Sixmile Cr. Headwaters—0.3 km from source)	5.6	14 C	6.8	0.005	Water	10%	33%	18%	39%
					Gut contents (<i>Simulium verecundum</i>)	6%	16%	4%	74%
No. 3 (Sixhundred Rd.—6.0 km from source)	2.1	15 C	7.6	0.39	Water	25%	25%	13%	37%
					Gut contents (<i>Simulium parnassum</i>)	27%	19%	8%	46%
No. 4. (Brooktondale—13.6 km from source)	3.5	20 C	8.0	0.7	Water	31%	34%	9%	26%
					Gut contents (<i>Simulium pictipes</i>)	77%	11%	4%	8%
No. 5 (Burns Road — 17.9 km from source)	3.8	21 C	----- NO DATA	-----	Water	68% ¹	6%	3%	23%

¹ Mainly empty frustules

more organic particles and fewer diatoms at Site 3 than at Site 4, even though the substrates were very similar. In general, the lower reaches had more total suspended material.

Maximum quantities of suspended material occurred in spring and consisted mainly of mineral fragments or material less than 5 μm . In summer and fall, diatoms made up a large portion of total suspended material in the lower reaches, sometimes up to 50% (e.g. November at Site 4). Plant fragments were numerous at forested headwater site (Site 2) in fall, and at Site 3 in spring.

Proportions of material in guts tended to correspond to proportions of materials carried in the stream, except that larvae commonly contained a higher percentage of diatoms. Usually, gut contents of different species at the same site were quite similar. At Site 1 in January, however, there was considerable difference between those of *Cnephia mutata* and *Prosimulium fontanum*.

Differences between the years were not analyzed, since duration of this study was short.

Organic content of the suspended material

Results of the analyses for organic content are shown in Table 8. Total organic content varied from 0.35–1.11 mg/l (7.9–24%). The highest percentage of organic matter in the suspended material did not coincide with the highest total amount of organic matter per liter.

The highest percentages of organic matter were found where organic fragments were common (e.g. Site 2 XI-4-70). Unfortunately, none of the water samples from Sixmile Creek chosen for analysis had a high proportion of diatoms. To show that large quantities of diatoms also increased the organic content, a result from a site similar to Site 4 (Taughannock Creek) is also shown. Low percentages were associated with large proportions of mineral fragments and/or material less than 5 μm (e.g. Site 2 IV-6-71, Site 3 I-26-71, Site 4 I-26-71, and II-25-71).

Digestion of diatoms

Diatoms examined 15 and 30 minutes after ingestion showed no visible change in appearance other than loss of mobility. After 40–60 minutes, the diatoms began to lose their golden-yellow color and became more transparent, revealing the striations on the frustules and the internal organelles. The clearing occurred first in diatoms near the gut wall. Within 3.5 hours, frustules became completely clear. This is of course much longer than the usual retention time (see Discussion). Non-ingested fresh diatoms which were killed in hot water and stored at room temperature did not clear for a least 48 hours. The clearing occurred at similar rates for *Cymbella* sp. in guts of larval *Simulium pictipes*, *Simulium tuberosum* and *Simulium jenningsi*.

DISCUSSION

Reliability of data

Reliability of data gathered for this work is limited by the method of estimating proportions of various materials in samples. Applied consistently, estimation of composition by area should give good comparative information. However, for absolute measurement of suspended material, estimation by microscopical measurement of area is less accurate than volumetric measurement or direct chemical analyses, but is more accurate than counting (Sladeckova, 1962). Neither area or volume estimates allow for differences in density. In Table 8, there is only a general agreement between the microscopical and chemical analyses.

Also, the particulate material examined was only a small fraction of the total material collected in water samples, which in turn were a very small percentage of flow of the stream at a particular time. Another aspect of the sampling problem was daily variability in stream discharge and concurrent

Table 8. Analysis of the organic content of material suspended in streams, Tompkins County, New York, 1970-1971.

Stream Site	Date	Composition of Suspended Material (estimated microscopically)			Total Suspended Material (mg/l)	Organic Content ¹	
		Diatoms	Mineral Fragments	Organic Fragments	Particles < 5 μ m	(mg/l)	(% dry wt.)
No. 2 (Hurd Rd. Stream)	XI-04-70	3%	15%	61%	21%	0.48	24%
	IV-06-71	3%	21%	39%	37%	0.44	9.7%
No. 3 (Sixmile Creek at Sixhundred Road)	1-26-71	5%	27%	15%	53%	0.41	8.7%
No. 4 (Sixmile Creek at Brooktondale)	1-26-71	1%	21%	12%	66%	0.70	9.6%
	11-25-71	3%	49%	21%	29%	1.11	7.9%
	VIII-25-70	60%	13%	6%	18%	0.35	14%
Taughannock Creek at Rabbit Run, 4.4 km below Waterburg, Romp Tompkins Co., N.Y.							

¹Micro method of Maciolek (1962). One replication per sample. When three replications were made with another sample, the coefficient of variation was 12%.

variability in content of suspended material. Sampling was done in periods of stable base flow when possible. Another approach would be to use automatic equipment capable of continuous sampling.

Interpretation of the stream samples

Factors such as type of terrain in the watershed, the nature of the substrate, degree of shading by streamside vegetation, and water depth and velocity can be used to explain the observed temporal and spatial variations in the quantity and composition of suspended material in the stream, as well as distribution of black fly larvae.

In forested headwater streams such as Site 2, fallen leaves are the main part of the organic material. Coarse leaf fragments ($>300\text{ }\mu\text{m}$) are especially important in the fall. These streams provide practically no diatoms because of heavy shading. In open headwater streams, such as Site 1 (which is on a south-facing slope), diatoms grew abundantly on trailing grass even in January. Both types of headwaters can produce large numbers of larvae, but of different species (i.e. *Prosimulium magnum* at Site 2; *Prosimulium fontanum*, *Cnephia mutata*, and several *Simulium* spp. at Site 1).

Changes seen at downstream sites in this study can be explained by a description of changes along a stream similar to that shown by Cummins (1977). The material from headwater streams is comminuted and diluted as it is carried downstream. Additional organic particles enter the stream from the vegetation bordering the stream, but this contribution becomes less important in relation to the volume of the stream as it coalesces and increases in discharge. Diatoms and other algae washed off of the substrate contribute more to organic content at this stage. Amount of algal growth varies with suitability of substrate and amount of sunlight. Sand and silt are continuously eroded from banks. Higher water velocities downstream tend to keep more material suspended.

Consistent with this picture of downstream changes, diatoms were more important at Site 3 and at Site 2, but organic particles still made up over 50% of the organic fraction. The large ($>300\text{ }\mu\text{m}$) leaf fragments common at Site 2 were not seen at Site 3. The bedrock substrate at Site 3 would certainly be suitable for algal growth, but diatoms may have been limited by shade from the forested banks. At Site 4, the substrate was bedrock, but was exposed to the sun with only a thin layer of water flowing over it. The suspended material there exceeded 10 mg/l and was often nearly 50% diatoms, especially during later summer months when discharge was low, illumination high, and floodwaters did not frequently scour the streambed. In early spring, with high water, more silt was present.

The data taken all on the same day (Table 7) support the idea of a trend toward fewer large particles and more diatoms downstream. Below Site 4, however, the diatoms were mostly empty frustules.

The presence of diatoms and organic particles increases the percentage of organic matter, but does not necessarily increase the total amount per liter. However, a small amount of organic matter in a pure form may be more beneficial than a larger amount heavily diluted with silt.

Interpretation of the gut contents

Proportions of materials in gut contents generally reflected proportions in the water, with little difference among larvae of different black fly species present at a given site. This indicates that feeding is indiscriminate. It was not uncommon, however, to find larvae that contained a higher proportion of diatoms than that found in the associated water. In the case of *Simulium pictipes* (Site 4 in April), this could be the result of more efficient feeding on the diatoms, which are larger than the silt particles (Kurtak, 1978). Also other fractions of gut contents may be digested, leaving behind only the insoluble diatom frustules and falsely inflating the percentage of diatoms.

At Site 1 in January, larvae of *Cnephia mutata* contained a much larger proportion of diatoms than did the water or larvae of *Prosimulium fontanum* at the same location. This can be explained by the

observation that larvae of *Cnephia mutata* often spend considerable time scraping material from the substrate rather than filter feeding (Kurtak, 1973).

No attempt was made to determine which components of gut contents are important in nutrition of black fly larvae, except to show that diatoms are in fact digested. The use of radioactive tracers would be one way to determine what portions of the gut content are assimilated.

It is clear that diatoms can be at least partly digested in the normal retention time, which is about one hour (Kurtak, 1978). Diatoms from larvae collected in natural habitats always appeared dead and clear since the larvae were held alive several hours before dissection.

Black fly larvae are known to ingest bacteria (Snoddy and Chipley, 1971) and there is evidence that bacteria may be an important food source in large rivers (Fredeen, 1960, 1964). No bacteria could be found in Sixmile Creek, but coliform bacteria are certainly present where the stream banks are densely populated. Truly rheophilic bacteria may also be present. These, however, are usually few in number and are difficult to culture (Hynes, 1970). Considerable numbers of bacteria may be associated with decomposing plant fragments in the water.

Black fly larvae also reportedly ingest particles as small as colloids (Wotton, 1976), but these particles require electron microscopical techniques to detect.

From the data it appears that the choice of a specific habitat by a black fly species has a strong influence on what kind of food the larvae will be exposed to. Larvae of *Simulium pictipes*, for example, which were characteristically found on bedrock substrates near waterfalls, usually contained large numbers of diatoms. The larvae of *Prosimulium magnum* on the other hand, usually contained large amounts of leaf fragments obtained in the small, shaded, forest streams where they lived. Another instance of direct relationship between habitat and food is reported by Carlsson *et al.*, (1977), who reported that larvae occurring below a lake in Sweden received nutrients in the form of fine particulate organic matter from the lake bottom. In the region of the present study, however, there were other species which occurred in a very wide range of habitats, such as *Simulium tuberosum* which Pinkovsky (1970) found at 85% of the sites he sampled in Tomkins County. Larvae of such a species would be exposed to a wide range of food.

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University of Alberta
Edmonton, Alberta, Canada T6G 2E3

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During Douglas Craig's term as Editor, we transferred from using a Selectric Composer to use of an electronic computer for setting up the issues. Although electronic computers may be expected to ultimately ease the task of production of copy for printing, initially a lot of work is involved, both by editor and operator. So, I am pleased to express my deep appreciation not only to Douglas, but also to Twyla Gibson, who acquired the necessary expertise to employ a computer for our work.

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Again, I take pleasure in thanking staff members of Printing Services, University of Alberta, for their excellent work in production of this volume.

**RHYSODINI OF THE WORLD PART II. REVISIONS OF THE SMALLER GENERA
(COLEOPTERA: CARABIDAE OR RHYSODIDAE)**

ROSS T. BELL

Department of Zoology

University of Vermont

Burlington, VERMONT 05401

JOYCE R. BELL

24 East Terrace

South Burlington, VERMONT 05401

Quaestiones Entomologicae

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This paper is the second of a series which will constitute a revision of the Rhysodini of the world and consists of revisions of all genera except for the four largest ones. Treated are: Leoglymmius Bell and Bell; Tangaroa Bell and Bell; Dhysores Grouvelle; Neodhysores Bell and Bell; Rhysodes Dalman; Kūpea Bell and Bell; Kaveinga Bell and Bell; Grouvellina Bell and Bell; Xhosores Bell and Bell; Yamatosa Bell; Shyrodos Grouvelle; Srimara Bell and Bell; Arrowina Bell and Bell; and Plesioglymmius Bell and Bell. Some of the genera have been redescribed, incorporating new information. Yamatosa NEW NAME replaces Yamatoa Bell 1977 which is preoccupied by Yamatoa Kiriakoff 1967

In Kaveinga Bell and Bell, four subgenera are recognized: Angekiva, NEW SUBGENUS, type-Kaveinga frontalis (Grouvelle), one sp., Australia; Ingevaka, NEW SUBGENUS, type-Kaveinga orbitosa (Broun), one sp., New Zealand; Vakeinga, NEW SUBGENUS, two spp., New Zealand, New Caledonia; Kaveinga (sensu stricto), 14 spp., New Guinea, Bismark Archipelago, Solomon Islands, Santa Cruz Island, Moluccas, and Mindanao.

In Plesioglymmius Bell and Bell, three subgenera are recognized: Plesioglymmius sensu stricto two spp., Sumatra, Borneo, Mindanao; Ameroglymmius NEW SUBGENUS, type-Plesioglymmius meridionalis (Grouvelle), three spp., South America, Cuba; Juxtaglymmius NEW SUBGENUS, type-Plesioglymmius jugatus NEW SPECIES, one sp., Java.

Rhysodes parvus Grouvelle, accidentally omitted from Part I, is assigned to Kaveinga (sensu stricto).

The following new species are described (and type localities indicated): Dhysores pan (ZAIRE, Kivu, Itombwe, 2300 m. Terr. Uvira, Nyalengwe); Dhysores liber (LIBERIA, crest of Mt. Nimba, 1400 m); Kaveinga fibulata (NEW BRITAIN, Rabaul); Kaveinga pignoris (SOLOMON IS., Bougainville, Kokure, 690 m) Kaveinga nudicornis (SOLOMON IS., Russell Is., Yandina); Kaveinga kukum (SOLOMON IS., Guadalcanal, Kukum); Kaveinga ulteria (SOLOMON IS., Santa Cruz Group, Reef Is.); Kaveinga lupata (NEW GUINEA, Mt. Kaindi, 16 km SW Wau); Kaveinga okapa (NEW GUINEA, Kamira, Eastern Highlands); Kaveinga marifuanga (NEW GUINEA, Marifuanga, Asaro-Chimbu Divide); Kaveinga histrio (PHILIPPINE IS., Mindanao, e. slope Mt. McKinley, 3300', Davao Prov.); Kaveinga strigiceps (Buru); Grouvellina gigas (MADAGASCAR, Chutes de la Mort); Grouvellina cuneata (MADAGASCAR, Tamatave and Forêt Alahakato); Grouvellina hova (MADAGASCAR, Tsaramainiandro); Grouvellina ranavalona, Grouvellina edentata, Grouvellina cooperi, Grouvellina montana (MADAGASCAR, only); Grouvellina radama (MADAGASCAR, Mahatsinjo); Grouvellina descarpentriesi (MADAGASCAR, Annanarivo); Grouvellina divergens (MADAGASCAR, Mt. d'Ambre); Grouvellina dentipes (MADAGASCAR, Fizonon); Grouvellina cinerea (MADAGASCAR, Perinet); Arrowina pygmaea (SRI LANKA, Dikoya); Plesioglymmius silus (PHILIPPINE IS., Mindanao, Zamboanga, Kabasalan); Plesioglymmius reichardt (VENEZUELA,

Suapure, Caura R.); *Plesioglymmius compactus (CUBA)*; and *Plesioglymmius jugatus (JAVA)*.

Cet article est la deuxième d'une série qui constitueront une revue taxonomique des Rhysodini du monde. La deuxième partie est composée des révisions taxonomiques de tous les genres sauf les quatre les plus grands. Les genres discutés sont: Leoglymmius Bell et Bell; Tangaroa Bell et Bell; Dhysores Grouvelle; Neodhysores Bell et Bell; Rhysodes Dalman; Kupea Bell et Bell; Kaveinga Bell et Bell; Grouvellina Bell et Bell; Xhosores Bell et Bell; Yamatosa Bell; Shyrodos Grouvelle; Srimara Bell et Bell; Arrowina Bell et Bell; et Plesioglymmius Bell et Bell.

Nous décrivons certains genres de nouveau, comprenant des renseignements nouveaux. Yamatosa NOUVEAU NOM remplace Yamatoa Bell 1977, car il est préoccupée de Yamatoa Kiriakoff 1967.

Nous divisons le genre Kaveinga Bell et Bell parmi quatre sous-genres: Angekiva NOUVEAU SOUS-GENRE, type-Kaveinga frontalis (Grouvelle), une sp., Australie; Ingevaka NOUVEAU SOUS-GENRE, type-Kaveinga orbitosa (Broun), une sp., Nouvelle Zélande; Vakeinga NOUVEAU SOUS-GENRE, type-Kaveinga setosa (Grouvelle), deux spp., Nouvelle Zélande et Nouveau Calédonie; Kaveinga (sensu stricto) 14 spp., Nouvelle Guinée, Archipel de Bismarque, Îles de Solomon, Îles de Saint Croix, Îles Moluques, et Mindanao.

Nous divisons le genre Plesioglymmius parmi trois sous-genres: Plesioglymmius sensu stricto, deux spp., Sumatra, Borneo, et Mindanao; Ameroglymmius NOUVEAU SOUS-GENRE, type-Plesioglymmius meridionalis (Grouvelle), trois spp., Amérique du Sud et Cuba; Juxtaglymmius, NOUVEAU SOUS-GENRE, type-Plesioglymmius jugatus NOUVELLE ESPÈCE, une sp., Java.

Par hasard, nous omîmes Rhysodes parvus Grouvelle de la première partie. C'appartient au genre Kaveinga, sous-genre Kaveinga (sensu stricto)

On décrit les espèces nouvelles que voici, en indiquant pour chacune la localité du spécimen type: Dhysores pan (ZAIRE, Kivu, Itombwe, 2300 m, Terr. Uvira, Nyalengwe); Dhysores liber (LIBÉRIA, crête du mont Nimba, 1400 m); Kaveinga fibulata (NOUVELLE BRETAGNE, RABAU): Kaveinga pignoris (ÎLES DE SOLOMON, Bougainville, Kokure, 690 m) Kaveinga nudicornis (ÎLES DE SOLOMON, ile Russell, Yandina); Kaveinga kukum (ÎLES DE SOLOMON, Guadalcanal, Kukum); Kaveinga ulteria (ÎLES DE SOLOMON, groupe Santa Cruz, ile Reef); Kaveinga lupata (NOUVELLE GUINÉE, Mt. Kaïndi, 16 km S.O. Wau); Kaveinga okapa (NOUVELLE GUINÉE, Kamira, Highlands de l'Est); Kaveinga marifuanga (NOUVELLE GUINÉE, Marifuanga, Asro-Chimbu Divide); Kaveinga histrio (ÎLES PHILIPPINES IS., Mindanao, versant est du mont McKinley, 3300', province du Davao); Kaveinga strigiceps (INDONÉSIE, Buru); Grouvellina gigas (MADAGASCAR, Chutes de la Mort); Grouvellina cuneata (MADAGASCAR, Tamatave et Forêt Alahakato); Grouvellina hova (MADAGASCAR, Tsaramainiandro); Grouvellina ranavalona, Grouvellina edentata, Grouvellina cooperi, Grouvellina montana (MADAGASCAR, sans localités spécifiées); Grouvellina radama (MADAGASCAR, Mahatsinjo); Grouvellina descarpentriesi (MADAGASCAR, Annanarivo); Grouvellina divergens (MADAGASCAR, mont d'Ambre); Grouvellina dentipes (MADAGASCAR, Fizonzo); Grouvellina cinerea (MADAGASCAR, PERINET); Arrowina pygmaea (SRI LANKA, Dikoya); Plesioglymmius silus (ÎLES PHILIPPINES IS., Mindanao, Zamboanga, Kabasalan); Plesioglymmius reichardt (VÉNÉZUELA, Suapure, Riv. Caura); Plesioglymmius compactus (CUBA); et Plesioglymmius jugatus (JAVA).

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INTRODUCTION

This paper, the second of a series of five, includes revisions of all the genera of Rhysodidae except *Clinidium* Kirby, *Rhyzodiastes* Fairmaire, *Omoglymmius* Ganglbauer, and *Pyxiglymmius* Bell and Bell. Some of the genera have been redescribed, incorporating new information. Otherwise, subtribal and generic descriptions have not been repeated; instead, the reader is referred to the appropriate pages in Part I (Bell and Bell 1978). A short list of additional references is added to supplement the extensive list in Part I.

SOURCES OF MATERIAL

The following abbreviations designate collections cited in this paper. The names in parentheses are the curators of the respective institutions.

- AIM Auckland Institute and Museum, New Zealand (K.A.J. Wise) ;
AMS Instituut voor Taxonomische Zoologie, Amsterdam, Netherlands (J. Duffels);
BMNH British Museum, Natural History, London (R. Pope);
BPBM Bernice P. Bishop Museum, Honolulu (G Samuelson);

- BSL Naturhistorisches Museum, Basel, Switzerland (W. Wittmer);
 CAS California Academy of Sciences, San Francisco, CA (D. Kavanaugh);
 CMP Carnegie Museum of Natural History, Pittsburgh, PA (G. Wallace);
 CNHM Field Museum of Natural History, Chicago, IL (H. Dybas);
 DSIR Department of Scientific and Industrial Research, Auckland, N.Z. (J. Watt);
 DY Daniel K. Young, Michigan State University, E. Lansing;
 LCC Lincoln College, Canterbury, N.Z. (R.M. Emberson);
 LEI Rijksmuseum von Natuurlijke Historie, Leiden, Netherlands (J. Krikken);
 MCZ Museum of Comparative Zoology, Cambridge, MA (J. Lawrence);
 MNHB Museum für Naturkunde der Humboldt-Universität, Berlin, DDR (F. Hieke);
 MNHN Muséum National d'Histoire Naturelle, Paris, France (A. Descarpentries);
 MRAC Musée Royal de l'Afrique Centrale, Tervuren, Belgium (P. Basilewsky);
 MZSP Museu de Zoologia da Universidade São Paulo, Brazil (U.R. Martins);
 NMNH United States National Museum of Natural History, Washington, D.C. (P. Hurd);
 NMNZ National Museum of New Zealand, Wellington (R.G. Ordish);
 SATO Masatako Satô, Nagoya, Japan.

SUBTRIBE LEOGLYMMIINA

Description. — Part I, 53. Only the one genus is known.

Leoglymmius Bell and Bell 1978

Type species. — *Rhysodes lignarius* Olliff 1885: 471.

Description. — Large, stout rhyssodine of somewhat caraboid appearance; with the characters of the subtribe; in addition, with the following: labrum with one pair of setae; one or two minute temporal setae, in isolated punctures posteromedial to eye; temporal lobe otherwise impunctate.

Pronotum slightly longer than wide, its sides curved, widest point anterior to middle; sides strongly convergent to apex; more moderately convergent to base; each side slightly sinuate anterior to hind angle; latter obtuse; median and paramedian grooves narrow, nearly linear, coarsely punctate, closed anteriorly, but widely open posteriorly; marginal groove single, slightly dilated, punctate; one or two marginal setae present; prosternum and propleura densely punctate; prosternum densely punctate, hairy.

Elytra relatively short and broad for a rhyssodine; humeral tubercle absent; basal scarp transverse, indistinctly defined; base of Stria VI continued anteromedially from humerus to base of scarp; elytral striae finely punctate, intervals nearly flat; Striae I–VII joined posteriorly in broad densely microsculptured depression; apical tubercle absent; two striae ventral to marginal Stria: upper one (Stria VIII) discontinuous, basal portion opposite metasternum, and apical portion opposite apical half of Sternum VI of abdomen; lower one (Stria IX) on border of epipleural rim, entire; metasternum punctate at sides, with one or more irregular longitudinal rows of punctures near midline; abdominal sterna coarsely punctate; female with densely microsculptured lateral areas on Sterna III–V, those of IV and V in form of shallow lateral pits.

Legs relatively long for a rhyssodine; setae of tarsi fewer, coarser than in other genera; male with ventral tooth on anterior femur; middle calcar small, acute, hind calcar shorter and less acute than middle one; female with acute inner process on middle tibia, simulating a calcar.

This genus is a phylogenetic relict. In a number of respects it is more like a normal carabid than are other rhyssodines. These include: a suture separating gena and mentum; broad bands of minor setae on the outer antennal segments; the absence of an apical tubercle; and the indistinctness of the basal scarp of the elytron.

We have assigned two additional species to the genus. *L. blackburni* (Grouvelle 1903) and *L. trichosternus* (Lea 1904). The only type specimens studied by us are a series of three *L. blackburni* in the Grouvelle collections (MNHN), all labelled as types. We hereby designate one of these types as

LECTOTYPE. This is a male, labelled "Victoria, Australia". **PARALECTOTYPES:** one female, same data as lectotype; one male, labelled "doit provenir d'Australie".

The three nominal species were not compared with one another in the original descriptions, and we have not investigated whether they are really separate species or merely three names for the same species. B.P. Moore will deal with the question in his forthcoming revision of the Australian rhyssodines.

SUBTRIBE DHYSORINA

Description. – Part I, 53.

Key to Genera. – Part I, 54.

Genus *Tangaroa* Bell and Bell 1978

Type species. – *Rhysodes pensus* Broun 1880.

Description. – Part I, 54. Only one species is known.

Tangaroa pensus (Broun) 1880)

Rhysodes pensus Broun 1880: 215.

Type material. – HOLOTYPE labelled: "TYPE, Mt. Mangaia, Broun Coll." (BMNH)

Another specimen, in the same collection, labelled COTYPE, is without locality data. In the original description, the type locality is given as Whangarei Harbour, and mention is made of an additional specimen from the Wairoa. In the main collection of the BMNH there is an additional TYPE specimen labelled "NEW ZEALAND:Broun". We have not had the opportunity to determine which, if any, of the above specimens represent the genuine type specimen.

Description. – Length 7–9 mm. Minor setae on Segments VI–X; antenna with basal setae on Segments V or VI–X; anterior tentorial pits large, V-shaped; labrum with two setae; orbital groove absent; temporal setae absent; marginal groove of pronotum single; precoxal carina absent; elytral Striae I–V impressed, punctate; Striae VI and VII effaced in anterior third; Stria VI not impressed, represented only by row of fine punctures; Stria VII with apical fifth impressed, remainder represented by fine punctures; metasternum relatively short, impunctate; abdominal sterna with scattered punctures; lateral pits not present in either sex; inner and outer spurs nearly equal on middle and hind tibiae; male with only slight development of calcaria, each represented by a swelling on anteromedial portion of apex of tibia; no other obvious secondary sexual characters.

This species is a large, rather stout rhyssodine, with a big pronotum and short, rather broad elytra. The absence of frontal grooves easily separates it from other New Zealand rhyssodines.

Range. – This species is confined to the North Island of New Zealand where it seems to be restricted to the northern half of the island. In addition to the type material, we have seen the following specimens: one female, Coroglen, 13-1-64, coll. P. Johns, "mixed podocarp & broadleaf forest" (LCC); one female, Kopu Rd., Coromandel Range, 30 Sept., 1967, coll. B. May (DSIR); one male, Little Barrier Island, coll. H. Swale (BMNH); one male, Parakao, Whangarei, 23-IX-1956, coll. R.A. Crowson (CAS); one female, Tamaha, North Auckland, no date, coll. C.E. Clarke (AIM); one male, Titirangi, 18-9-1915 (BMNH); one male, Whangarei, Mar. 18-20, 1931, coll. E.S. Gourley (DSIR).

Genus *Dhysores* Grouvelle 1903

(Fig. 1-8)

Type species. – *Rhysodes thoreyi* Grouvelle 1903.*Description.* – Part I, 54.

Type species. – *D. thoreyi* of South Africa occurs from sea level to an elevation of 6000 feet (Brinck 1965). All the remaining species live in tropical Africa, where they are confined to montane forests. They are allopatric, and, with the possible exception of *D. quadriimpressus*, each is limited to a single mountain range. Adults of all the species are much alike externally, but males show clear-cut differences in genitalia. The tropical species do not form clear-cut groups among themselves, suggesting that each of them may have evolved from a relict population of *D. thoreyi*, assuming that the latter species was once able to spread northward during a period of cooler and moister climate.

KEY TO SPECIES

- | | | | |
|--------|---|---|-----|
| 1 | Pronotum with discal striole plus basal impression 87% of length of pronotum; prosternum with well-developed precoxal carinae..... | <i>Dhysores pan</i> new species, p. | 382 |
| 1' | Discal striole plus basal impression 50–80% of length of pronotum; precoxal carinae rudimentary or absent..... | | 2 |
| 2 (1') | Anterior tentorial pits and prefrontal pits both large and deep, in form of prominent rectangle..... | <i>Dhysores quadriimpressus</i> (Grouvelle), p. | 384 |
| 2' | Anterior tentorial pits small; prefrontal pits varied from large to minute | | 3 |
| 3 (2') | Pronotum narrow – sides nearly parallel, base and apex only slightly narrowed; small, narrow beetles, length 4.6–5.0 mm | <i>Dhysores liber</i> new species, p. | 384 |
| 3' | Pronotum broadened at middle – sides strongly curved, base and apex distinctly narrowed; larger, broader beetles, length 5.2–6.5 mm | | 4 |
| 4 (3') | Discal striole plus basal impression 50% of length of pronotum; humeral tubercle reduced (Fig. 8) | <i>Dhysores thoreyi</i> (Grouvelle), p. | 384 |
| 4' | Discal striole 60–80% of length of pronotum; humeral tubercle larger, more prominent (Fig. 7) | | 5 |
| 5 (4') | Prefrontal pit deep, larger than anterior tentorial pit.. <i>Dhysores rhodesianus</i> (Brinck), p. | | 385 |
| 5' | Prefrontal pit shallow, equal to or smaller than anterior tentorial pit..... | <i>Dhysores basilewskyi</i> (Brinck), p. | 385 |

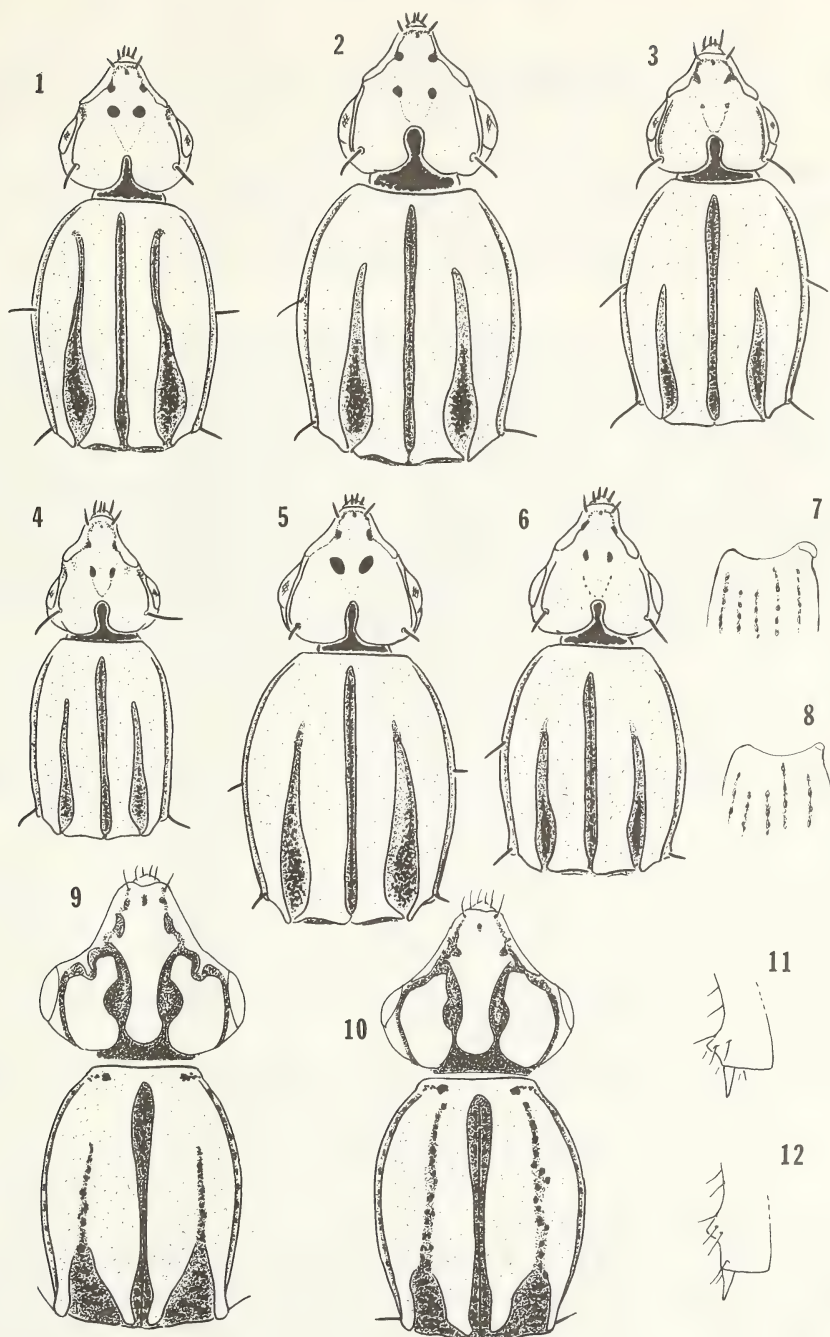
Dhysores pan new species

(Fig. 1)

Type material. – HOLOTYPE male, labelled: “Kivu: Itombwe; 2300 m., Terr. Uvira, Nyalengwe, N. Leleup, XI, 1959” (MRAC). The locality is in eastern Zaire, west of Lake Kivu.

Description. – Length 5.9 mm. Anterior tentorial pits small, indistinct; prefrontal pits large, oval, not at all oblique; frontal grooves scarcely visible; two pairs of postlabial setae; pronotum relatively elongate, its margin not sinuate anterior to hind angle, latter obtuse; base of pronotum conspicuously sinuate medial to hind angle; hind angle obtuse; discal striole (including basal impression) about 87% of length of pronotum, rather sharply divided into basal impression 25% of length of pronotum, and long and sinuate discal striole proper; striae convergent to anterior fourth of pronotum, slightly divergent more anteriorly; one marginal seta; prosternum with long precoxal carina, extended over half the distance between coxal and anterior margin; striae VI and VII nearly complete, but faded near humeral tubercle.

This species is easily recognized by the long discal striole and well-developed precoxal carinae.



Figures 1 – 12. Fig. 1-8, Genus *Dhysores*; Fig. 1-6, Head and pronotum, dorsal aspect; Fig. 1, *D. pan* new species; Fig. 2, *D. quadriimpressus* (Grouvelle); Fig. 3, *D. thoreyi* (Grouvelle); Fig. 4, *D. liber* new species; Fig. 5, *D. rhodesianus* (Brinck); Fig. 6, *D. basilewskyi* (Brinck); Fig. 7, 8, Base of right elytron, dorsal aspect; Fig. 7, *D. basilewskyi* (Brinck); Fig. 8, *D. thoreyi* (Grouvelle); Fig. 9-12, Genus *Rhysodes*; Fig. 9, 10, Head and pronotum, dorsal aspect; Fig. 9, *R. sulcatus* (Fabricius); Fig. 10, *R. comes* (Lewis); Fig. 11, 12, Hind tibia, male, apical portion. Fig. 11, *R. sulcatus* (Fabricius); Fig. 12, *R. comes* (Lewis).

Dhysores quadriimpressus (Grouvelle)

(Fig. 2)

Rhysodes quadriimpressus Grouvelle 1910: 325.

Type material. — LECTOTYPE (here designated) male, labelled: "Usumbara, Nguelo" (MNHN). The locality is at present in BURUNDI, formerly German East Africa. Arrow (1942) and Hincks (1950) erroneously attributed it to Tanganyika. PARALECTOTYPE one female, same data as lectotype (MNHN).

Description. — Length 6.0–6.8 mm. Anterior tentorial pits large, round, equal in size to prefrontal pits, the four in form of a conspicuous square; frontal grooves relatively distinct, though very shallow; two pairs of postlabial setae; pronotum relatively narrow anteriorly, basal impressions uniformly deep, about 70% of length of pronotum, narrowed uniformly anteriorly; hind angles denticulate; one marginal seta; Stria VI reduced to fine row of punctures, its anterior fourth effaced; Stria VII impressed, its anterior fourth effaced.

This species is recognized by the enlarged anterior tentorial pits. In addition to the type material, a specimen from Tanzania possibly belongs to this species. It is a female labelled "Tanzanie: Mts. Uluguru, Kinola, for. transition, alt. 1500–1750 m., arbres morts 6–13-VI-71, coll. L. Berger, N. Leleup, J. Debecker" (MRAC). This specimen differs from the type material only in lacking the marginal seta of the pronotum. It may not be conspecific with the specimens from Burundi, but a final decision will have to await study of genitalia of males from both localities.

Dhysores liber new species

(Fig. 4)

Type material. — HOLOTYPE male, labelled: "LIBERIA, Crest of Mount Nimba 1400 meters, 15-VIII-1966. coll. E.S. Ross, K. Lorenzen" (CAS). PARATYPE female, same data (CAS).

Description. — Length 4.6–5.0 mm. Narrower and more cylindrical than other members of the genus; anterior tentorial pits small, punctiform; prefrontal pits shallow, small, elongate oval; frontal grooves distinct though very shallow; one pair of postlabial setae; pronotum with margin nearly parallel, slightly sinuate anterior to scarcely denticulate hind angles; discal striole (including basal impression) about 70% of length of pronotum; basal impression shallow; discal striole almost straight; marginal seta of pronotum absent; precoxal carina short; Stria VI represented by fine punctures, extended almost to humerus; Stria VII very fine, shallow, represented anteriorly by row of fine punctures.

This is the only species of *Dhysores* known from West Africa. It can be recognized by its small size, narrow form, and nearly parallel-sided pronotum.

The paratype differs from all other *Dhysores* in that the minor setae begin on antennal segment IV.

Dhysores thoreyi (Grouvelle 1903)

(Fig. 3,8)

Rhysodes thoreyi Grouvelle 1903: 125.

Type material. — not examined by us. According to Grouvelle (1903) the type series is in the Cape Town Museum. The species is represented by abundant material (BMNH and other museums).

Description. — Length 5.0–6.0 mm. Microsculpture better developed than in related species, body less shining; anterior tentorial pits relatively distinct, oblique; prefrontal pits shallow, small, punctiform, in some specimens virtually obliterated; frontal groove very shallow to almost absent; two pairs of postlabial setae; pronotal margin with short sinuation anterior to hind angle, latter rectangular or nearly so, minutely denticulate; base markedly sinuate medial to hind angle; discal striole, including basal impression, about 50% of length of pronotum; discal striole anterior to basal impression narrow, shallow; marginal seta present; precoxal carina absent; elytra more narrowed at base than in other *Dhysores*, humeral tubercle smaller (Fig. 8); Stria VI reduced to row of minute punctures not extended to humerus; Stria VII effaced in anterior third and interrupted opposite apical striole, gap with several large setigerous punctures; penis with tip tapered to narrow point on left side.

This species is easily recognized by the reduced humeral tubercles, narrow, oblique anterior tentorial pits, markedly reduced or obsolete prefrontal pits, and short discal striae. *Dhysores thoreyi* is known only from the Union of South Africa, where it is found in Natal Province and the eastern Cape Province, from sea level to 6000 feet in altitude (Brinck 1965).

Brinck (1965) provides a map of the localities.

Dhysores rhodesianus (Brinck 1965)

(Fig. 5)

Rhysodes (Dhysores) rhodesianus Brinck 1965: 467–468.

Type material. – According to Brinck, the type series includes many adults in the Transvaal Museum, from RHODESIA: Mt. Selinda Forest, 9-17.4, 1956, leg. G. Van Son and L. Vari. We have not seen this material, but have studied a PARATYPE female, labelled: “RHODESIA: Chirinda Forest, Dec., 1901, leg. G.A.K. Marshall” (BMNH).

Description. – Length 5.2–6.6 mm. Anterior tentorial pits punctiform, small but distinct; prefrontal pits large, oval, somewhat oblique; frontal grooves evident though very shallow; two pairs of postlabial setae; pronotal margin sinuate anterior to minutely denticulate hind angle, base markedly obliquely sinuate medial to hind angle; discal striae including basal impression about 80% of length of pronotum; anterior portion of discal striae very shallow; striae convergent anteriorly except extreme anterior ends parallel to one another; marginal seta present; prosternum without trace of precoxal carina; Stria VI and VII almost entire, effaced only in anterior tenth of elytron; penis with apex triangular, in form of short, obliquely truncated apical lobe.

The elongate discal striae give this species a resemblance to *Dhysores pan*, from which it is easily separated by the sinuation anterior to the hind angles and absence of a precoxal carina. The well-developed obliquely oval prefrontal pits are unique in *Dhysores*, and recall those of *Neodhysores*.

In addition to the paratype we have seen one male specimen in MRAC labelled “Chirinda (misspelled?) F., XII-52, vSon”.

Dhysores basilewskyi (Brinck 1965)

(Fig. 6,7)

Rhysodes (Dhysores) basilewskyi Brinck 1965: 468–469.

Type material. – HOLOTYPE male, labelled: “RUANDA, Astrida, 1750 m., 22-2-1953, coll. P. Basilewsky” (MRAC). PARATYPE female, same data as type (MRAC).

Description. – Length 5.0–6.5 mm. Anterior tentorial pits scarcely evident; prefrontal pits medium-sized, oval, moderately deep, not oblique; mentum with one pair of postlabial setae; lateral margins of pronotum distinctly sinuate anterior to denticulate hind angles; sinuation medial to hind angle shorter than in related species; discal striae, including basal impression 60–75% of length of pronotum; discal striae convergent anteriorly, very shallow near apex; marginal seta of pronotum absent from most specimens (present unilaterally in one specimen); Stria VI and VII completely effaced in anterior third of elytron; apex of penis much more obtuse than in *Dhysores thoreyi* and *Dhysores rhodesianus* males.

The denticulate hind angles, shorter discal striae, and the absence of precoxal carinae separate this species from *Dhysores pan*. The reduced anterior tentorial pits separate it from *Dhysores quadriimpressus*, while smaller prefrontal pits, the shorter discal striae and the more extensive abbreviation of Striae VI and VII are the most obvious differences from *Dhysores rhodesianus*.

In addition to the type material, a series of six specimens from Zaire appear to belong to this species. These are labelled “B. CONGO, 42 mi. N. of Kapona, 1520 m., I-13-58, coll. E.S. Ross, R.E. Leech” (CAS).

Genus *Neodhysores* Bell and Bell 1978

Type species. – *Neodhysores seximpressus* Bell and Bell 1978

Description. – Part I, 56.

KEY TO SPECIES

- 1 Pronotum relatively short; length/greatest width 1.28; antennal Segment XI as wide as long*Neodhysores seximpressus* Bell and Bell, p. 386
- 1' Pronotum elongate, length/greatest width 1.43; antennal Segment XI much longer than wide*Neodhysores schreiberi* (Vulcano and Pereira), p. 386

Neodhysores seximpressus Bell and Bell 1978

Type material. – Part I, 56. The type locality is Nova Teutonia, Santa Catarina State, Brazil.

Description. – Part I, 56.

Neodhysores schreiberi (Vulcano and Pereira) 1975a)

Rhysodes schreiberi Vulcano and Pereira 1975a: 219.

Type material. – One type and one paratype in the collection of the describers; we have not studied the types. The type locality is Belo Horizonte, Minas Gerais State, Brazil.

Description. – Vulcano and Pereira 1975a: 219.

SUBTRIBE RHYSODINA

Description. – Part I, 56.

Key to Genera. – Part I, 57.

Genus *Rhysodes* Dalman 1823

Fig. 9-12

Type species. – *Cucujus sulcatus* Fabricius 1787.(= *Rhysodes exaratus* Dalman 1823, by monotypy)

Synonym. – *Epiglymmius* Lewis 1888: 79 (Type species *Cucujus sulcatus* Fabricius 1787, designated by Hincks, 1950)

Description. – Part I, 58. Prosternum without precoxal carina.

KEY TO SPECIES

- 1 Pronotum relatively short, length/greatest width 1.1; discal striole of pronotum well separated from anterior margin*Rhysodes sulcatus* (Fabricius), p. 387

- 1' Pronotum more elongate, length/greatest width 1.2; discal striole almost reaching anterior margin of pronotum..... *Rhysodes comes* (Lewis), p. 388

Rhysodes sulcatus (Fabricius 1787)

(Fig. 9,11)

Cucujus sulcatus Fabricius 1787: 165.

Rhysodes exaratus Dalman 1823: 93.

Rhizodes europaeus Ahrens 1814: 1.

Type material. – Not located.

Description. – Length 6.8–8.3 mm. Antennal Segment XI slightly less than twice as long as wide; stylet more than 0.33 of length of cone; clypeus slightly emarginate in midline anteriorly; narrow oblique bridge connecting clypeal rim to median lobe, interrupting clypeal groove anterior to each anterior tentorial pit; frontal grooves oblique, sinuate; median lobe distinctly narrowed between openings of frontal pit, medial emargination of temporal lobe relatively wide and deep; anterolateral projection of temporal lobe relatively approximate to antennal rim; latter with distinct narrow brace directed posteromedially from its posterior end, opposite distinct emargination in temporal lobe; orbital groove relatively dilated; base of mentum in form of distinctly projecting lobe in lateral view; mentum with numerous short setae in form of “beard” in male, only scattered setae in female; gular grooves with anterior halves indistinct.

Pronotum relatively short and broad, length/greatest width 1.1, both apex and base more narrowed than in *R. comes*; discal striole plus basal impression 80% of length of pronotum; basal impression about 33% of length of pronotum; hind angles acute; lateral margins parallel in basal fifth, divergent just anterior to hind angles; lateral margin deeply sinuate anterior to hind angles; precoxal rim with short stub representing rudimentary precoxal carina; punctures of prosternum each with prominent seta.

Elytral intervals flatter than in *R. comes*; Stria VII with five to seven setae near apex; apical striole with three to four setae.

Anterior and middle tibiae hairy beneath, more densely so in male; all tibiae hairy medially in both sexes; middle tibia of male with conspicuous lateral setae, that of female with few setae; hind calcar large, pointed, only slightly dorsad to spur (Fig. 11).

Range. – Widely distributed in Europe, but now confined to small, scattered relict areas, probably because centuries of intensive use of wood have restricted the development of overmature trees. Dajoz (1975) gives a detailed account of the recent and nineteenth century distributions. The westernmost localities are in the Pyrenees of southern France. The species also occurs in Italy, Germany, Poland, Ukraina, Yugoslavia, Rumania, and Sweden. We have seen specimens (NMNH) from Asiatic Turkey, from the Taurus Mountains near Adana. Dajoz also lists it from the Caucasus. It does not now occur in Britain, but is known from subfossil remains (Kelley and Osborne, 1965; Buckland and Kenward, 1972) the most recent remains being from about 1000 B.C.

Bionomics. – Despite its rarity, *Rhysodes sulcatus* is better known ecologically than any other species of Rhysodini. Dajoz (1975) and Burakowsky (1975) have summarized previous work and have added their personal observations about the species. Tiberghien (1969) gives a detailed account of *R. sulcatus* in the Pyrenees. Considering the accounts of these authors together, it is evident that *Rhysodes sulcatus* depends for its survival on the presence of very large, old trees. It is seemingly indifferent to the species of tree. It has been reported from fir (*Abies alba* Mill.), spruce (*Picea excelsa* (Law.) Lk., beech (*Fagus silvatica* L.), aspen (*Populus tremula* L.), and other species of poplar (*Populus* spp.). It is confined to dead wood, but apparently is not particular about the state of the wood, occurring in badly decayed logs, as well as dry, hard ones and even charred stumps in a burned area. It is known from both standing and fallen trunks. Waga (1841, quoted by Grouvelle, 1903) collected specimens from the roots of poplar (*Populus*) at depths down to two meters.

Tiberghien (1969) found *Rhysodes sulcatus* specimens associated with myxomycetes in burnt stumps of fir (*Abies*), while Dajoz (1975) collected them in stumps of beech (*Fagus*) which were infested with oyster fungus (*Pleurotus ostreatus*). Burakowsky (1975) states that Trella (1926, 1939) found numbers of adults hibernating in galleries of the larvae of *Ceruchus chrysomelinus* Hochw. (Coleoptera, Lucanidae) in a rotten fir (*Abies*) trunk.

Burakowsky (1975) has described and illustrated larvae and pupae as well as illustrating many details of structure of adults. He believes that two years are required to complete metamorphosis, as shown by the presence of two size classes of larvae during the summer. Larvae, unlike adults, live in well-defined galleries. These are in the moister, more decayed parts of wood. The older parts of the gallery, behind the larvae, are tightly packed with wood fragments.

Rhysodes comes (Lewis 1888)

(Fig. 10,12)

Epiglymmius comes Lewis 1888: 79.

Type material. – LECTOTYPE (here designated) male, labelled: "JAPAN: Nikko, Aug. 10-18, 1881, coll. G. Lewis" (BMNH). PARALECTOTYPES, two females, JAPAN: Sapporo, Aug. 5-6, 1880, coll. G. Lewis (BMNH).

Description. – Length 6.5–8.0 mm. Antennal Segment XI more than twice as long as wide; cone elongate, stylet less than 33% as long as cone; clypeus truncate anteriorly, not emarginate; bridge from median lobe to margin of clypeus incomplete or lacking; frontal grooves almost longitudinal, in form of acute angle with antennal grooves; median lobe narrowed opposite frontal pits; medial emargination of temporal lobe smaller and shallower than in *Rhysodes sulcatus*; temporal lobe without distinct anterolateral projection; antennal rim without posteromedial brace; temporal lobe scarcely emarginate opposite antennal rim; antennal groove nearly straight; orbital groove relatively narrow, in contact with antennal groove at slight angle anterior to eye; mentum with "beard" in male, scattered setae in female; base of mentum less prominent in lateral view than in *Rhysodes sulcatus*; gular groove complete.

Pronotum longer and narrower than in *Rhysodes sulcatus*, length/greatest width about 1.20; base and apex not as strongly narrowed as in *Rhysodes sulcatus*; basal impression less than 0.25 of total length of pronotum; discal striae elongate, more than twice as long as basal impressions, extending almost to anterior margin of pronotum; hind angles slightly obtuse; sides of pronotum not parallel anterior to hind angles; lateral sinuation much shallower than in *Rhysodes sulcatus*; precoxal carina absent; punctures of prosternum without evident setae.

Elytral intervals more convex than in *Rhysodes sulcatus*; elytron with one seta at tip of Stria IV, three to six at tip of Stria VII; and with or without one in apical striae.

Male with about four ventral setae on anterior femur, and with or without one ventral seta on middle femur; female without ventral setae on femora; tibiae with only a few medial setae; middle tibia without lateral setae; calcar of hind tibia very small, very obtusely angled, distinctly dorsad to spur (Fig. 12).

Range. – Japan and Siberia. In Japan, known from the following islands; HONSHU: Nikko (the lectotype); Sanno-Toge, Oku-Nikko (DY); Yumato, Iwase (DY); Ooda Iima-Gnu (Mie Pref.) (SATO); KYUSHU: Wakamatsu (DY); HOKKAIDO: the paralectotypes. The Siberian specimen, the first record from the U.S.S.R., is from Kongaus, Siberia, coll. Cockerell, August, 1923. The locality is on Nakhodka Bay, about 75 miles east of Vladivostok.

Genus *Kupea* Bell and Bell 1978

Type species. – *Clinidium arcuatum* Chevrolat 1873a.

Description. – Part I, 58. Only one species is known.

Kupea arcuatus (Chevrolat 1873a)

Clinidium arcuatum Chevrolat 1873a: 216.

Rhysodes aterrimus Broun 1880: 214 (nec Chevrolat 1873a)

Rhysodes brouni Lewis 1888: 79.

Type material. – *Rhysodes arcuatus*: HOLOTYPE male, no locality, labelled: “*Rhyz. antarcticus*”, as far as we can determine an unpublished name (MNH); *R. aterrimus* Broun; LECTOTYPE – sex not determined, labelled: “NEW ZEALAND: Tairua” (BMNH–Broun Collection). PARALECTOTYPES two specimens, sex not determined (BMNH–1 in general collection, the other in Broun Collection). *Rhysodes brouni* Lewis was a substitute name for *Rhysodes aterrimus* Broun, preoccupied by *Rhysodes aterrimus* Chevrolat 1873a.

Description. – With characters of genus; length 5.0–8.0mm. Pronotum with angular seta but without marginal setae; prothorax with several postcoxal setae; precoxal carina absent; Stria II with one to two setae near tip; Stria IV with one seta near base and another near tip; Striole with one or more setae; Stria VII with about five setae in apical fifth; middle tibia with prominent acute calcar, directed ventroanteriorly; calcar of hind tibia smaller than that of middle tibia, acute, located entirely dorsad to apex of tibia.

This species is easily recognized among New Zealand Rhysodini by the form of the head, with the narrow, parallel-sided median lobe separated on either side from the temporal lobe by a linear frontal groove.

Range. – The North Island of New Zealand and nearby coastal islands. The locality records indicate that it occurs throughout the North Island. In addition to the type material, we have seen specimens from the following localities: one female, Boatmans Reef (BMNH); one female, Hunua, coll. Drury (BMNH); three males, two females, Kawau I., 6-1902, coll. J.J. Walker (BMNH); one male, three females, Little Barrier I., coll. H. Swale, 1913 (BMNH); one female, Mararainui, Bay of Plenty, May, 1928, coll. A.E. Brookes (DSIR); two males, Maud I., 1-6-3-53, coll. E.S. Gourley (DSIR); two males, one female, Mayar I., Dira Bay, 11 Nov. 55, coll. J.C. Watt (DSIR); one female, Mayar I., Te Ohineiti, 14 Nov. 55, coll. J.C. Watt (DSIR); one female, Okauai, Maramara, Waikato, 1-11-1931, coll. A.E. Brookes (DSIR); one female, Oruru, 6-9-10, coll. A.E. Brookes (DSIR); one male, Papakura, Auckland, 26-12, 1926, coll. A.E. Brookes (DSIR); one male, Paparoa, coll. A.E. Brookes (DSIR); one female, Plummerton (MCZ); one male, one female, Pollok, Auckland, 7-1-64, coll. P. & M. Johns (LCC); one female, Ratanihipiki, Taranaki (BMNH); one female, Springs Junct. Br., 5-V-1977, coll. R.M. Emberson (LCC); three males, one female, Titirangi, 21-3-1913 (Broun Colln.) (BMNH), same locality, 1913-14, coll. T. Broun (DSIR), same locality, 5-10-27, coll. E.S. Gourley (DSIR); one male, Waikanae, IX-1930, coll. G.V. Hudson (BMNH), one male, same locality, Sept. 5, 1938, “GVH” (DSIR); two females, Waipoua, 4-12-63, Kauri bark, coll. P.M. Johns (LCC); one female, Waitakeri, 31-12-14, coll. A.E. Brookes (DSIR); six males, four females, Wellington (may refer either to province or city) (BMNH); one male, Whangarei, Western Hills, 13-IX-1956, coll. R.A. Crowson (CAS); one male, Whangarei, 18-20,3,31, coll. E.S. Gourley (DSIR); one male, Whangarei Dist., Maunga Karama, 13-2-1926, coll. E. Fairburn (DSIR); two males, two females, Wilton’s Bush, 2-11-44, coll. G.V. Hudson (BMNH), same locality, 6-11-20 (DSIR).

Genus *Kaveinga* Bell and Bell 1978

(Fig. 13-51)

Type species. – *Rhysodes abbreviatus* Lea 1904.

Description. – Antennal stylet absent except in one undescribed Australian species; antennal Segment V without minor setae, latter on Segments VI–X, but confined to more distal articles in specimens of a few species; labrum with two setae; medial margin of temporal lobe curved or oblique, not closely parallel to margin of median lobe; temporal and medial lobes entirely separated or else in contact for short distance posteriorly; orbital groove, if present, terminated near posterior margin of eye; pronotum in most species with complete, entire paramedian grooves (in *Kaveinga orbitosa*) paramedian groove represented by row of very coarse punctures; precoxal carinae present on prosternum; humeral tubercle well developed; middle and hind tibiae each with one spur.

In many species, the tip of the median lobe is supported ventrally by a slender pillar. This feature is easily seen in species such as *K. histrio*, in which the median lobe is markedly raised above the pronotum but would require dissection to verify in those species in which the head is low and wide. One specimen of *K. abbreviata* had the tip of the median lobe broken off, revealing a pillar. Perhaps this feature will prove to be an invariable characteristic of *Kaveinga*. The pillar is entirely posterior to the frontal pit, so that the latter forms a transverse passageway beneath the median lobe (Fig. 37,47).

This markedly diverse and divergent genus differs from its relatives in having only two labral setae, and in having precoxal carinae. It differs from *Rhysodes* in having distinct humeral tubercles and in having the orbital groove ending at or anterior to the posterior margin of the eye. It differs from *Kupea* in having the paramedian grooves complete or nearly so, and in not having the margins of the medial lobe and temporal lobes parallel and close to one another along the entire length of the head.

Kaveinga ranges from New Zealand, New Caledonia and the Santa Cruz Islands through Australia and New Guinea to Buru in the Moluccas and Mindanao in the Philippines.

Phylogeny. – The described species of *Kaveinga* are included in four subgenera. The subgenera can be grouped into pairs which appear to represent major phyletic lines. Within each pair, the two genera are allopatric. In *Vakeinga* and *Kaveinga (sensu stricto)*, the paramedian grooves are broad, deep, entire, and impunctate. *Vakeinga* occurs in New Zealand and New Caledonia, while *Kaveinga (sensu stricto)* occupies the remainder of the range of the genus. The second pair of subgenera appear less certainly related to one another, though they are linked together by having the pronotal grooves coarsely punctate. *Angekiva*, confined to Australia, have the paramedian grooves entire, curved, and nearly linear. *Ingevaka*, confined to New Zealand, have the paramedian grooves represented by a series of very coarse punctures.

There is an undescribed species from Australia which does not fit into the above subgenera, and may require erection of a fifth subgenus, although it may prove to be an aberrant species of *Angekiva*. This species will be described by Dr. Moore in his monograph of the Australian Rhysodini. This species was mistakenly regarded as *Rhysodes lignarius* Olliff by Grouvelle. (The true *R. lignarius* belongs to *Leoglymmius*.) There are two specimens of the undescribed species in the MNHN, one labelled “Richmond R., N.S. Wales”, the other without specific locality data. We have also seen two specimens in the MCZ collection, one from the McPherson Range, Queensland, and the other from rain forest north of Dunoon, New South Wales.

The undescribed species differs from all other *Kaveinga* in the presence of an antennal stylet. Both sexes have a ventral tooth on the anterior femur, though that of the female is very small. The pronotum is like that of *Angekiva*, except that the paramedian grooves are scarcely punctate.

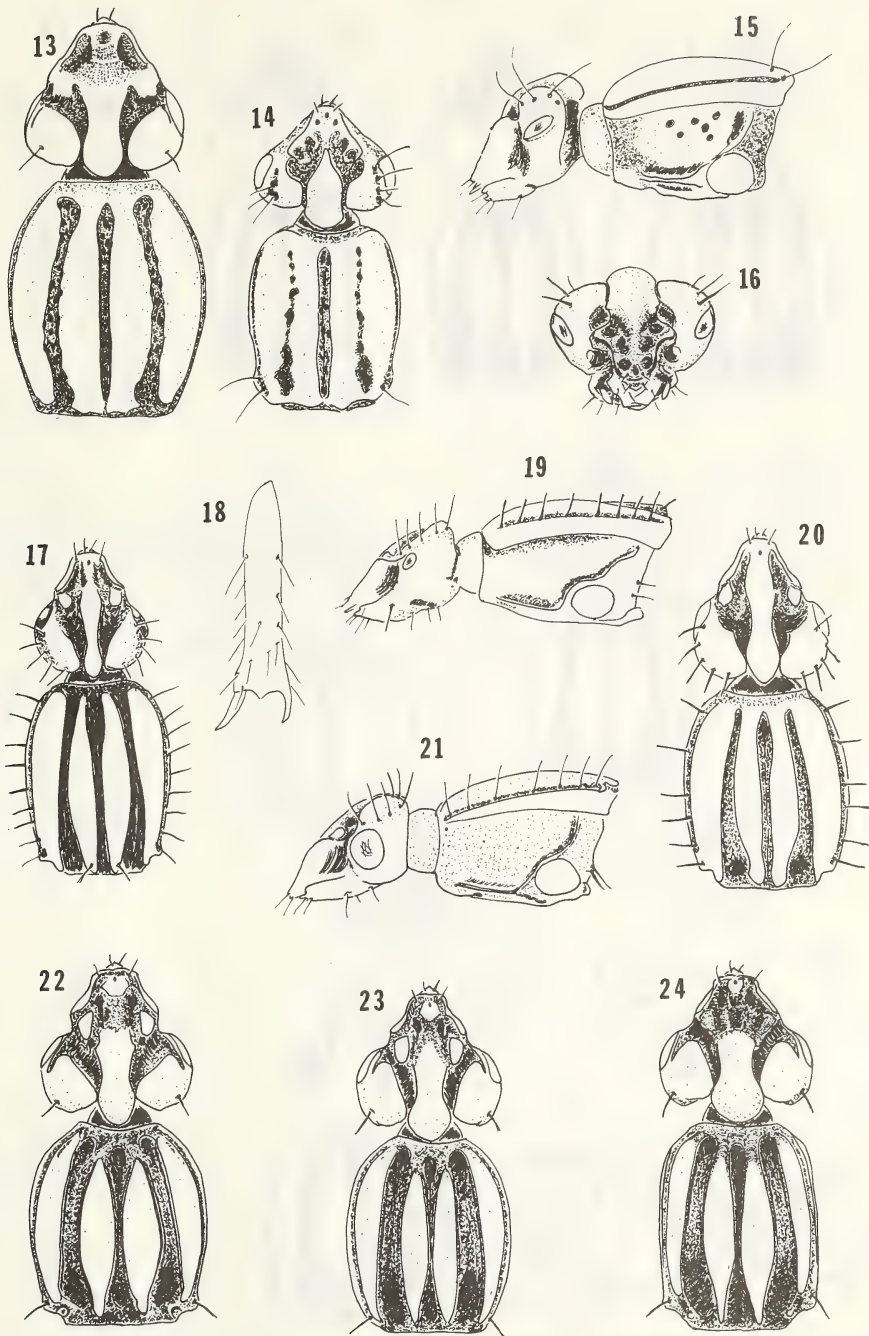
KEY TO SUBGENERA

1	Paramedian grooves entire, open both anteriorly and posteriorly	2
1'	Paramedian groove incomplete, closed both anteriorly and posteriorly, represented by row of very coarse punctures	<i>Ingevaka</i> new subgenus, p. 394
2 (1)	Paramedian grooves linear, markedly curved, punctate; pollinosity, if present, limited to punctures.	<i>Angekiva</i> new subgenus, p. 390
2'	Paramedian grooves not linear, not markedly curved, without punctures, pollinosity continuous from base to apex	3
3 (2')	Temporal setae numerous; marginal setae of pronotum numerous, in form of continuous row	<i>Vakeinga</i> new subgenus, p. 395
3'	Temporal setae 1–3; marginal setae 0–3, when present, limited to anterior and posterior ends of marginal groove	<i>Kaveinga (sensu stricto)</i> , p. 397

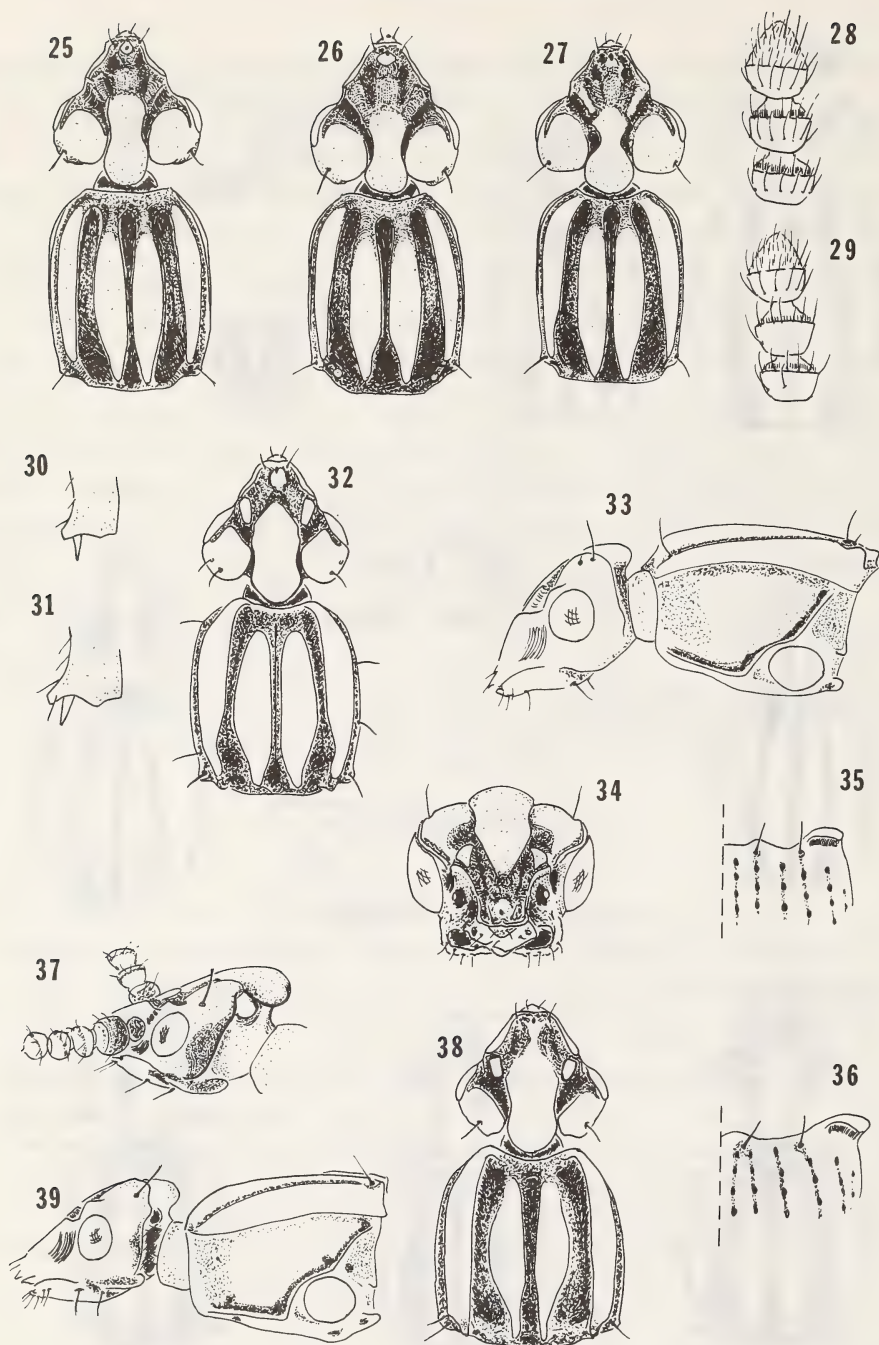
Subgenus *Angekiva* new subgenus

Type species. – *Rhysodes frontalis* Grouvelle 1903.

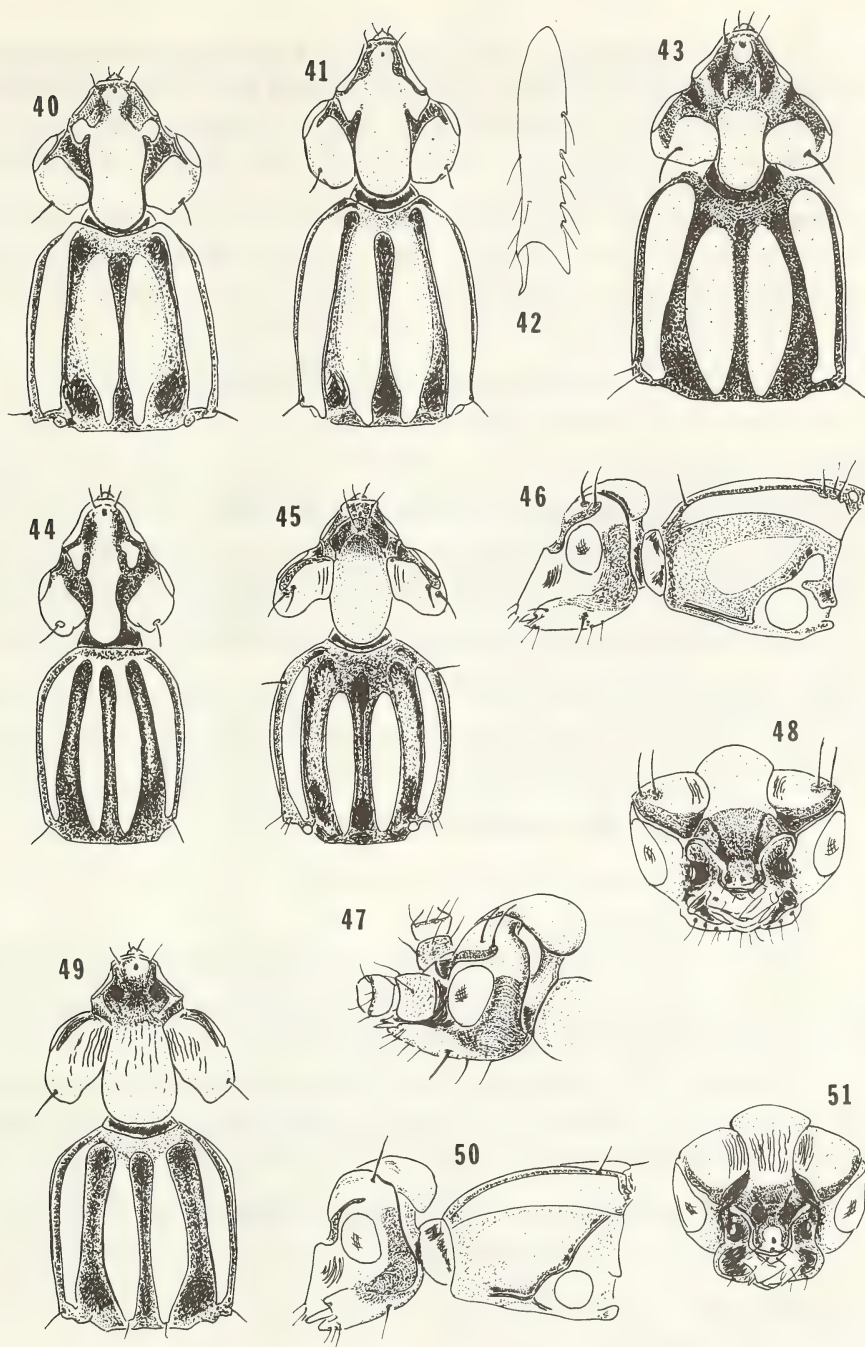
Description. – Antennal Segment XI without stylet; antennal segments not pollinose; median groove of pronotum coarsely punctate; paramedian grooves curved, linear except at base; complete, coarsely to sparsely punctate; pollinosity restricted to punctures, or else absent; angular seta present or absent; marginal setae absent; prosternum coarsely punctate, punctures either generally distributed or else confined to margins of precoxal carinae; elytral striae glabrous; femora glabrous; femur of anterior leg without ventral tooth in either sex (in species where both sexes are known); middle tibia without lateral serrulation, and without lateral setae.



Figures 13 – 24. Fig. 13-21, Genus *Kaveinga*; Fig. 13, Head and pronotum, dorsal aspect, *K. (Angekiva) frontalis* (Grouvelle); Fig. 14-16, *K. (Ingevaka) orbitosa* (Broun); Fig. 14, Head and pronotum, dorsal aspect; Fig. 15, Head and pronotum, lateral aspect; Fig. 16, Head, anterior aspect, antennae omitted; Fig. 17-19, *K. (Vakeinga) lusca* (Chevrolat); Fig. 17, Head and pronotum, dorsal aspect; Fig. 18, Middle tibia; Fig. 19, Head and pronotum, lateral aspect; Fig. 20,21, *K. (V.) setosa* (Grouvelle); Fig. 20, Head and pronotum, dorsal aspect; Fig. 21, Head and pronotum, lateral aspect; Fig. 22-27; Head and pronotum, dorsal aspect; Fig. 22; *K. (Kaveinga) abbreviata* (Lea); Fig. 23, *K. (K.) fibulata*, new species; Fig. 24, *K. (K.) kukum* new species.



Figures 25 – 39. Fig. 25, *K. (K.) pignoris* new species; Fig. 26, *K. (K.) ulteria* new species; Fig. 27, *K. (K.) nudicornis* new species; Fig. 28,29, Antennal Segments IX-XI; Fig. 28, *K. (K.) pignoris* new species; Fig. 29, *K. (K.) nudicornis* new species; Fig. 30,31, Hind tibia, male, apical portion; Fig. 30, *K. (K.) pignoris* new species; Fig. 31, *K. (K.) ulteria* new species; Fig. 32-35 *K. (K.) cylindrica* (Arrow); Fig. 32, Head and pronotum, dorsal aspect; Fig. 33, Head and pronotum, lateral aspect; Fig. 34, Head, anterior aspect, antennae omitted; Fig. 35, Base of right elytron, dorsal aspect; Fig. 36-39, *K. (K.) lupata* new species; Fig. 36, Base of right elytron dorsal aspect; Fig. 37, head, posterolateral aspect; Fig. 38, Head and pronotum, dorsal aspect; Fig. 39, Head and pronotum, lateral aspect.



Figures 40 – 51. Fig. 40, *K. (K.) okapa* new species; Fig. 41, *K. (K.) marifuanga* new species; Fig. 40,41 Head and pronotum, dorsal aspect; Fig. 42, Middle tibia, *K. (K.) marifuanga* new species; Fig. 43,44, Head and pronotum, dorsal aspect; Fig. 43, *K. (K.) occipitalis* (Grouvelle); Fig. 44, *K. (K.) parva* (Grouvelle); Fig. 45-48, *K. (K.) histrio* new species; Fig. 45, Head and pronotum, dorsal aspect; Fig. 46, Head and pronotum, lateral aspect; Fig. 47, Head, posterolateral aspect; Fig. 48, Head, anterior aspect, antennae omitted; Fig. 49-51, *K. (K.) strigiceps* new species; Fig. 49, Head and pronotum, dorsal aspect; Fig. 50, head and pronotum, lateral aspect; Fig. 51, head, anterior aspect, antennae omitted.

The curved, linear, punctate paramedian grooves are diagnostic of this subgenus. The type species is the only described species. However, we have also studied two unnamed species which will be described by Dr. Moore. One species has large eyes which are deeper than long, a complete orbital groove, and a very shallow, glabrous postantennal groove. This species is known from Malanda, north Queensland (MCZ), and from Mt. Kairi, Queensland (CAS).

The second species resembles *K. frontalis* in having the eye reduced, the orbital groove absent, and the postantennal groove deep. It differs in having the median lobe of the head very slender, strongly constricted near the middle, the median pit of the clypeus very small, and the eye circular. This species is represented by a specimen from Mt. Spurgeon, northern Queensland (MCZ).

Kaveinga (Angekiva) frontalis (Grouvelle 1903) NEW COMBINATION
(Fig. 13)

Rhysodes frontalis Grouvelle 1903: 104–105.

Type material. – HOLOTYPE male, labelled: “TASMANIA” (MNHN).

Description. – Length 7 mm. Antennal Segment XI obtuse, 1.5 times longer than wide; minor setae on Segments VI–X; basal setae on Segments VI–X. Head as wide as long; clypeal setae absent; clypeus with enlarged median pit; clypeal grooves dilated; postclypeal grooves incomplete, so median lobe is connected to parafrontal bosses; median lobe relatively broad, about 0.25 of width of head; median lobe only slightly constricted anteriorly; postantennal grooves deep, pollinose; one temporal seta; orbital groove reduced to minute vestige; eye deeper than long, apparently slightly reduced (in holotype very heavily pigmented so that it is difficult to see its outlines).

Pronotum longer than wide, oval, widest near middle, its base and apex both strongly narrowed; sides strongly curved; angular seta absent; prosternum and propleura coarsely punctate.

Elytral setae restricted to apex of Stria VII; metasternum coarsely punctate; abdominal Sterna entirely coarsely punctate; male with very small ventral tooth on anterior femur; female unknown.

Subgenus *Ingevaka* new subgenus

Type species. – *Rhysodes orbitosus* Broun 1880

Description. – Antennal Segment XI without stylet; antennal segments not pollinose; median groove of pronotum coarsely punctate; paramedian grooves nearly straight, coarsely punctate; impressed posteriorly, reduced to row of punctures anteriorly; closed both anteriorly and posteriorly; angular seta present; marginal seta varyingly developed, most often absent; anterior lateral pits absent; elytral striae shallow, glabrous; anterior femur of male with ventral tooth in some specimens, absent from others; females without ventral tooth on anterior femur; tibia of middle leg without lateral serration or lateral setae.

The incomplete paramedian grooves are the mark of this subgenus. The short, high, transverse head resembles those of certain species of *Kaveinga (sensu stricto)*, surely as a result of convergent evolution.

Subgenus *Ingevaka* contains only one species, which is confined to the North Island of New Zealand.

Kaveinga (Ingevaka) orbitosa (Broun 1880) NEW COMBINATION
(Fig 14–16)

Rhysodes orbitosus Broun 1880: 215–216.

Rhysodes luscus auct., nec Chevrolat 1875.

Rhysodes eminens auct., nec Broun 1880

Lewis (1888) wrongly supposed this species to be the male of *R. eminens* Broun (*Rhysodes luscus* Chevrolat).

Type material. – We have studied a specimen labelled as cotype in BMNH. It is without locality data. We have not located any other type material. According to the original description the type material was collected at Whangarei Harbour.

Description. — Length 4–5 mm. Body very short and transverse for a rhysodine; head short, strongly transverse, about twice as wide as long; clypeal setae present; clypeus separated from median lobe by pollinose impression; clypeus with three conspicuous pits; clypeus continuous laterally with antennal lobes; each antennal lobe with two medial braces; median lobe short, high, in form of raised crest (Fig. 16), its anterior end acutely pointed, its posterior end rounded; temporal lobes markedly transverse, their medial margins fitted into cavities on sides of median lobe; three to four temporal setae, each inserted in conspicuous pit (in many specimens pits fused in form of one elongate depression; in other specimens pits separate, in one specimen pits fused on left lobe and separate on right lobe); eye markedly reduced, about twice as long as wide, with about sixty ommatidia; cornea thickened, without facets.

Pronotum subquadrate, widest anterior to middle; sides slightly curved and distinctly sinuate well anterior to posterior angles; marginal groove distinct; prosternum with wide groove medial to each precoxal carina; prosternum impunctate; propleuron with a few very coarse punctures.

Elytra very short, convex, inflated; stria punctures very coarse; Stria I with two setae in apex; Stria II and IV with setae both at apex and at base; in many specimens with continuous series of setae in either II or IV, in a few with continuous series in both striae; apical striole with several setae; apex of Stria VII with several setae; metasternum concave in midline, but not truly sulcate; metasternum with median line of coarse punctures, a cluster of punctures anterior to each hind coxa, and with five to six large lateral punctures; abdominal sterna III–V each with narrow transverse, almost uniseriate band of punctures; calcar of male small and pointed.

Variation. — Seven of the nine males examined had well-developed ventral teeth on the anterior femora. Two males differ strikingly in lacking the teeth. One of these is from Little Barrier Island (BMNH), and the other (NMNH) is without locality data. One female from Waitakiri (DSIR) has numerous marginal setae on the pronotum, while in all other specimens the marginal setae are restricted to one near the angular setae or are entirely absent. The variations listed above are quite comparable to specific differences seen in other groups of Rhysodini, so it is possible that future work will show that there are several species of *Ingevaka* in New Zealand.

Range. — We have seen specimens with the following locality data: AUCKLAND: one male, Little Barrier I., coll. H. Swale, 1913-117 (BMNH); one male, Okauia, Matamata, Waikato, A.E. Brookes Colln., 11-3-1923 (DSIR); one female, Omahuta, Kauri forest, Jan. 1972, coll. G.W. Ramsay (DSIR); one male, Waimatenui, Hobson Co., C.E. Clarke Colln. (AIM); one male, one female, Wainui Bay, saddle, Kaea Northland, 4-Nov-67, coll. J.I. Townsend (DSIR); one female, Waipoua, 15 June 66, coll. J.I. Townsend (DSIR); one male, one female, Whangarei, Heads, C.E. Clarke colln. (AIM); one male, Warkworth, The Dome, 21 Oct. 1962, coll. J.C. Watt (DSIR); one female, Whangarei, Tiraki, A.E. Brookes colln, 8-9-23 (DSIR); one male, Whangarei, Western Hills, 13-IX-1956, coll. R.A. Crowson (CAS); HAWKES BAY(?): two females, Waipoua S.F., VI-9, 13-66, coll. J.C. Watt (DSIR); one female, Waitakiri, 26-10-14(380), T. Broun A.E. Brookes colln. (DSIR).

Subgenus *Vakeinga* new subgenus

Type species. — *Rhysodes setosus* Grouvelle 1903

Description. — Antennal Segment XI without stylet; antennal Segment I finely pollinose above; remaining antennal segments without pollinosity; minor setae on Segments VI–X; head with distinct parafrontal bosses; four to five temporal setae; orbital groove absent or vestigial; grooves of pronotum deep, pollinose, impunctate; paramedian grooves relatively broad, open anteriorly and posteriorly; inner carinae not abbreviated anteriorly; marginal groove complete; angular seta present; five to nine marginal setae; prosternum, propleura impunctate; several postcoxal setae on prothorax; elytral striae without pollinosity; elytron with several setae in apices of Striae I and VII, and complete series in striae II and IV (setae sparse or absent from middle third of Striae II and IV in some specimens; female with small lateral pits in Sterna IV–V; femora glabrous; anterior femur without ventral tooth in either sex; middle tibia with row of setae on lateral aspect, but without lateral serrulation.

This subgenus is similar to the allopatric *Kaveinga* (*sensu stricto*) in the structure of the prothorax. It differs from the latter in having many lateral setae, and in lacking lateral serrulation on the middle tibia (Fig. 18). The deep, entire, pollinose, impunctate paramedian grooves are the best means of separating it from the sympatric *Ingevaka*. *Vakeinga* has one species in New Zealand, and one in New Caledonia.

KEY TO SPECIES

- 1 Eye large, round, its diameter about half depth of head; pronotum without setae at bases of inner carinae..... *Kaveinga setosa* (Grouvelle), p. 396

- 1' Eye very small, oblique, its diameter less than 0.2 depth of head; one seta on each inner carina near its posterior end *Kaveinga lusca* (Chevrolat), p. 396

Kaveinga (Vakeinga) setosa (Grouvelle 1903) NEW COMBINATION
(Fig. 20,21)

Rhysodes setosus Grouvelle 1903: 108.

Type material. – According to Grouvelle, the type was in the Oberthur collection. We could not locate it in MNHN. However, the description and the locality are sufficient to recognize the species.

Description. – Length 4.8–5.0 mm. Minor setae well developed on antennal Segments VI–X; basal setae absent; head slightly longer than wide; median lobe narrowed between eyes, its posterior end spatulate, pointed; anteromedial margin of temporal lobe strongly angulate midway between eye and medial angle; orbital groove vestigial; eye large, nearly round, its diameter over half depth of head; cornea faceted, unpigmented.

Pronotum moderately elongate, length/greatest width 1.20, widest near middle, sides strongly curved; inner pronotal carina without seta near base; five to six marginal setae; prosternum with pair of pits between precoxal carinae; elytra narrow, cylindrical; striae coarsely punctate.

This species is easily distinguished from the next by: fully developed eyes, absence of seta from the base of the inner carina, broader median lobe, shorter head and pronotum, and absence of basal setae from the antennae.

Range. – New Caledonia. The only specimens we have seen are two males and one female labelled: “NEW CALEDONIA, Forêt de Thi, Hanna, VII-16-1958, leg. B. Malkin” (CNHM).

Kaveinga (Vakeinga) lusca (Chevrolat 1875) NEW COMBINATION
(Fig. 17–19)

Rhysodes luscus Chevrolat 1875: 183.

Rhysodes eminens Broun 1880: 215.

Type material. – *R. luscus*: not located by us. *R. eminens*: “COTYPE”, sex not recorded, without specific locality data in Broun Collection (BMNH). Broun states that the original specimens were collected at Whangarei Harbour. We do not know whether or not there are additional type specimens. Grouvelle (1903) states that he had studied types of *R. luscus* and had concluded that *R. eminens* and *R. orbitosus* were conspecific, but this is not so. The original description of *R. luscus* agrees with that of *R. eminens* and not *R. orbitosus*.

Description. – Length 4.7–6.6 mm. Minor setae sparse on Segment VI, well developed on Segments VII–XI; basal setae on Segments VI–X, head distinctly longer than wide, median lobe narrower than in *K. setosa*, convex, constricted between eyes; anteromedian margin less distinctly angulate than in *K. setosa*; orbital groove absent; eye markedly reduced and modified; cornea oblique, twice as long as deep; cornea not faceted, clear in some (presumably younger) specimens, markedly pigmented in other specimens; ommatidia about twenty, grouped in round central disc much smaller than cornea.

Pronotum distinctly elongate, length/greatest width about 1.25; sides distinctly curved; inner carina with seta near base; seven to nine marginal setae; precoxal carinae markedly developed, extended to anterior margin of prosternum; each precoxal carina bounded medially by wide groove; these grooves closely approximated at middle of length, separated by median carina; no pits between precoxal carinae; elytra moderately broad, somewhat flattened; striae less coarsely punctate than in *K. setosa*.

The reduced, oblique eyes distinguish this species from *K. setosa*. *K. lusca* differs markedly from *K. (Ingevaka) orbitosa*, with which it was formerly considered conspecific. *K. lusca* has complete paramedian grooves, a low, elongate head and temporal lobes which are not in close contact with the median lobe.

Range. – Confined to the North Island of New Zealand, where it is widespread. We have seen specimens from the following localities: one male, one female, Herekino, Manganui Co., G.E. Clarke Colln. (AIM); one female, Mt. Hikurangi, 4000, 17-I-64, coll. P. Johns (LCC); one male, Motu R., 12-11-28, A.E. Brookes Colln. (DSIR); one male, two females, Mt. Maungapohatu, 914-1219 m., 3-Mar-71, coll. J.I. Townsend (DSIR); one male, Parkanae Opononi, 17-XI-1968, Hokianga Co., coll. K.A.J. Wise (AIM) one male, Pukerui Hills, Whangarei 21-11, coll. G. Given (DSIR); two males, Tepaki Coastal Park, North Cape, 7 Feb 1975, coll. J.C. Watt (DSIR); three males, five females, Tepaki Coastal Park, S. Pandora, 7 Feb 1975, coll. S.E. Nichols (DSIR); one male, Unuwhao trig., Spirits Bay, 20-28-VIII-1957, coll. J.C. Watt (DSIR); three males, Waimatenui, Hobson Co., C.E. Clarke Colln. (AIM); two females, Wainui Bay, saddle, Kaea, 4 Nov 62, coll. J.I. Townsend (DSIR); two males, three females, Waipoua, VI-66-, X-67, coll. J.C. Watt and VI-66, coll. J.I. Townsend (DSIR); one male, one Whanaki North Whangarei Co., 15-XI-1968, coll. K.A.J. Wise (AIM); one male, one female, Whangarei, 8-9-23, A.E. Brookes Colln. (DSIR); one female, Whangarei, Western Hills, 13-X-56, coll. R.A. Crowson (CAS).

Subgenus *Kaveinga sensu stricto* Bell and Bell 1978

Type species. – *Rhysodes abbreviatus* Lea 1904

Description. – Antennal Segment XI without stylet; antennal Segment I pollinose above; in adults of most species pollinose bands or spots on more distal segments; in adults of few species, pollinosity confined to Segment I; minor setae on Segments VI-X; parafrontal boss either distinct or else fused to median lobe; one to three temporal setae; pronotum with grooves deep, entire, pollinose; parameginal grooves broad, open anteriorly and posteriorly; marginal groove complete; angular seta present or absent; 0-three marginal setae, when present, located near anterior and/or posterior angles of pronotum; prosternum, propleura impunctate; postcoxal setae absent; elytral pollinosity and setae variably developed; abdominal sterna of female without enlarged lateral pits; anterior femur without ventral tooth in either sex; femora in most species with dorsal and ventral pollinose strips (in a few species reduced or absent); middle tibia with row of lateral setae, with a minute tooth between each pair of setae, the teeth in form of serrate lateral margin in anterior or posterior aspect (Fig. 42); serration indistinctly developed in *K. strigiceps* and some specimens of *K. abbreviata*.

Members of this markedly diverse and divergent subgenus differ from those of all other subgenera in having the lateral margin of the middle tibia serrulate. In addition, females differ from those of *Vakeinga* in lacking lateral pits from the abdomen of the female, and in having fewer setae and better developed pollinosity. *Kaveinga (sensu stricto)* occupies most of the range of the genus, but is absent from New Caledonia and New Zealand. In Australia it is limited to northern Queensland.

Phylogeny. – The species *Kaveinga (sensu stricto)* comprise three distinct groups. The members of Group I have deep, pollinose elytral striae and subcarinate to carinate intervals. The abdominal sterna are transversely sulcate. This group includes *K. abbreviata* of Australia, *K. fibulata* of New Britain and the *K. pignoris* complex of the Solomon Islands and Santa Cruz Islands. In this group, all species except *K. abbreviata* have the pronotum elongate.

The species in Group II have the striae shallow or not impressed and without pollinosity. The abdominal sterna each have a transverse row of punctures with an interruption at the midline. This group includes *K. parva*, *K. cylindrica*, *K. lupata*, *K. okapa*, and *K. marifuanga*, all from New Guinea. In this group, all species except *K. parva* have the pronotum scarcely elongate.

The species of Group III have the head very short and broad, and the margin the pronotum raised. They show marked convergence in head structure with subgenus *Ingevaka* of New Zealand. The elytral striae are deep and pollinose, and the intervals are narrow and convex to carinate. The abdominal sterna are transversely sulcate, and the pronotum is not elongate. This group includes *K. occipitalis* of New Guinea, *K. histrio* of Mindanao, and *K. strigiceps* of Buru.

An important question is whether each of these groups is an independent phyletic line or whether either Group I or Group II is simply a collection of primitive (plesiomorphic) species. To answer this question, it is necessary to decide the character states of the elytral striae and intervals in the common ancestor of the subgenus. The other subgenera of genus *Kaveinga* have the elytral striae deep but not pollinose, and the elytral intervals convex but not carinate. In other words, they are intermediate between those of Groups I and II. Of all the species of *Kaveinga (sensu stricto)*, only *K. parva* of Group II approaches the other subgenera in elytral structure.

One possible hypothesis would be that *K. parva* is primitive in the structure of its elytra, and that the remaining species have departed from the ancestral condition in two directions. In the remainder of Group II, the striae have become more shallow and the punctures finer, while in Groups I and III the striae have become deepened and pollinose, and the intervals have become subcarinate to carinate.

A second possible hypothesis is that pollinose striae and subcarinate intervals characterized the ancestral species, and that members of Group II have undergone a secondary loss of pollinosity and a reduction of the depth of the striae. Several lines of evidence seem to us to point to the second hypothesis. Significant are the geographical distributions of the two character states, evidence supplied by pollinosity of the femora, and that of sculpture of the abdominal sterna. The species characterized by shallow, non-pollinose striae and flat elytral intervals form a compact group in New Guinea, while those characterized by carinate intervals and pollinose striae are much more widely distributed and much more varied in structure. This suggests that Group II represents a local radiation within New Guinea. Reduced striation is a conspicuous feature of the species of *Omoglymmius* (*sensu stricto*) and *Omoglymmius* (*Nitiglymmius*) in New Guinea also, suggesting that it is in some way an adaptation to local conditions.

Most species of *Kaveinga* (*sensu stricto*) have conspicuous pollinose bands on the femora. Some species of Group II are characterized by traces of these bands, while in others, the bands are entirely absent. This suggests that the ancestor of the subgenus had such bands, and that they are in the process of being lost in the species of Group II, an idea consistent with the theory that the common ancestor of the subgenus was more like Group I than Group II.

Members of subgenera other than *Kaveinga* (*sensu stricto*) have the abdominal sterna with the punctures in broad bands. Members of *Kaveinga* (*sensu stricto*) either have the punctures of each sternum in a uniseriate transverse row (Group II) or else have a transverse sulcus on each sternum (Groups I,III). Transverse sulci may contain punctures, though they are in many specimens concealed by the pollinosity. We postulate that the development of sulci resulted in alignment of the punctures in uniseriate rows, and that a subsequent reduction in sculpture of the body in Group II resulted in the disappearance of the sulci, leaving behind the uniseriate rows of punctures.

If it is accepted that deep, pollinose striae, subcarinate intervals, partly pilose femora, and sulcate abdominal sterna were features of the ancestral species of *Kaveinga* (*sensu stricto*), then the possibility exists that Group I is merely a collection of primitive (plesiomorphic) species, and is not a single phyletic line. *K. fibulata* and the *K. pignoris* complex are small, narrow species which appear to be closely related to one another. *K. abbreviata*, however, differs from the preceding species in its shorter, broader form, and in the tendency for the abdominal sulci to be interrupted. It may really be as close to the species in Groups II and III as it is to the remainder of Group I.

In Group II, the most isolated species is *K. parva*, in which the striae are distinctly impressed and the pronotum is elongate. If deep pollinose striae and carinate intervals are regarded as primitive within the subgenus, then this species is the least modified in the group. The four remaining species have the striae reduced to rows of punctures, or, at most, with a few of the inner striae slightly impressed. They also have the pronotum, at most, slightly longer than wide. They form two pairs of closely related species. *K. cylindrica* and *K. lupata* inhabit the middle altitudes of the mountains of the extreme eastern part of New Guinea. *K. okapa* and *K. marifuanga* form a similar pair in the east central mountains. The distribution is markedly similar to that of the New Guinea species of *Omoglymmius* subgenus *Nitiglymmius*. It suggests for each genus that the range of an ancestral species was split, and two daughter species evolved, one in the east central mountains, and the other in the eastern mountains. This was followed by a further fragmentation of range, in which each daughter species became divided into two species. Still later, local barriers disappeared, leading to sympatry within each mountain region. In

Group II of *Kaveinga*, the more specialized pair of species inhabits the east central mountains, while in *Nitiglymmius*, the reverse is true, with the less specialized pair on the east central mountains.

Group III has one species in New Guinea and two species in the islands further west. *K. histrio* of Mindanao and *K. strigiceps* of Buru are much more specialized than *K. occipitalis* of New Guinea, and are obviously related to one another. *K. occipitalis* stands out from other New Guinea *Kaveinga* in having carinate elytral intervals and a transversely sulcate abdomen. Its resemblances are to the members of Group I, especially *K. abbreviata*, rather than to Group II. Its presence on New Guinea requires confirmation, as it is known only from the holotype, collected over a century ago, though there is no concrete reason to doubt the authenticity of the label.

KEY TO SPECIES

1	Head distinctly longer than deep, at least slightly longer than wide.....	2
1'	Head deeper than long, much wider than long.....	12
2 (1)	Elytral striae deeply impressed, continuously pollinose; elytral intervals markedly convex, at least the outer ones carinate.....	3
2'	Elytral striae shallowly impressed or not impressed; striae not pollinose; interval flat*or nearly so.....	8
3 (2)	Pronotum relatively short, broad, length/greatest width 1.1 or less	
 <i>Kaveinga abbreviata</i> (Lea), p.	400
3'	Pronotum elongate, length/greatest width 1.2–1.3	4
4 (3')	Hind angle of pronotum rounded; parafrontal boss well developed	
 <i>Kaveinga fibulata</i> new species, p.	401
4'	hind angle of pronotum obtuse; parafrontal boss reduced or absent	5
5 (4')	Basal setae of antennal Segments VI–X well developed, forming transverse row on each segment (Fig. 28); median lobe shallowly sinuate on either side	6
5'	Basal setae of antennal Segments VI–X reduced, each segment with setae limited to lateral margins (Fig. 29); median lobe deeply sinuate on either side.....	
 <i>Kaveinga nudicornis</i> new species, p.	403
6 (5)	Strial punctures very coarse, each puncture about 0.5 as wide as interval; hind calcar of male relatively longer and less obtuse (Fig. 31)	
 <i>Kaveinga ulteria</i> new species, p.	402
6'	Strial punctures less coarse, each puncture about 0.3 as wide as an interval; hind calcar of male shorter, obtuse (Fig. 30).....	7
7 (6')	Outer carina of pronotum without basal knob; pronotum shorter, its lateral margins more curved	
 <i>Kaveinga pignoris</i> new species, p.	402
7'	Outer carina with distinct basal knob; pronotum more elongate, its sides more nearly straight	
 <i>Kaveinga kukum</i> new species, p.	402
8 (2')	Pronotum elongate, length/greatest width about 1.25; striae distinctly impressed.....	
 <i>Kaveinga parva</i> (Grouvelle), p.	403
8'	Pronotum not elongate; length/greatest width 1.0 to 1.1; striae not impressed or only inner striae impressed.....	9
9 (8')	Parafrontal boss separate from median lobe; lateral margins of median lobe shallowly emarginate.....	10
9'	Parafrontal boss partly fused to median lobe; lateral margins of median lobe straight.....	11
10 (9)	Humeral tubercle not exerted (Fig. 35); elytra narrow, cylindrical	

 <i>Kaveinga cylindrica</i> (Arrow), p.	403
10'	Humeral tubercle exerted (Fig. 36); elytra broader, somewhat flattened.....	
 <i>Kaveinga lupata</i> new species, p.	404
11 (9')	Suborbital tubercle prominent; median lobe partly or entirely separated from clypeus by pollinose area; transverse rows of punctures on abdominal sterna III-V not interrupted.....	
 <i>Kaveinga okapa</i> new species, p.	405
11'	Suborbital tubercle very small; median lobe broadly continuous with clypeus; transverse rows of punctures on abdominal sterna III-V broadly interrupted medially	
 <i>Kaveinga marifuanga</i> new species, p.	406
12 (1')	Temporal lobe transverse posteriorly; humeral tubercle exerted.....	
 <i>Kaveinga occipitalis</i> (Grouvelle), p.	406
12'	Temporal lobe with posterior margin strongly oblique in dorsal view; humeral tubercle not exerted	13
13 (12')	Orbital grooved extended posterior to eye; median lobe smooth; temporal lobe with few rugae.....	
 <i>Kaveinga histrio</i> new species, p.	407
13'	Orbital groove ending opposite eye; median and temporal lobes rugose	
 <i>Kaveinga strigiceps</i> new species, p.	407

Kaveinga (sensu stricto) abbreviata (Lea 1904)

(Fig. 22)

Rhysodes abbreviatus Lea 1904: 79-80

Type material. — Lea cites "Cairns, Q." as the type locality and the type depository as the Macleay Collection. We have not been able to see the type specimen but have seen a long series from the type locality with the following data: 11 males, 10 females, Queensland, Upper Little Mulgrave river, S.W. Cairns, 23,27-VII and 3-VIII-69, coll. J.E. Tobler; one female, Cairns, 1952, coll. J. Sedlacek (all CAS).

Description. — Length 5.2-6.7 mm. Antennal Segment I pollinose dorsally; Segments II-V each with narrow pollinose band; basal setae reduced, well developed only on Segments VIII-X or IX-X, in some specimens with few on more proximal segments; head slightly longer than wide; clypeus broadly separated from median lobe by band of pollinosity; parafrontal boss triangular, as wide as long, widely separated from median lobe; sides of median lobe broadly sinuate; orbital groove as long as eye, slightly dilated; temporal lobes slightly wider than long, oblique, anteromedial margins converging posteriorly; medial angle rounded, scarcely overlapped by median lobe; one temporal seta; pollinosity of postorbit well developed, extended to eye ventrally; temporal lobe with slight overhang in lateral view; suborbital tubercle and gular ridge absent.

Pronotum relatively short, broad, length/greatest width 1.10; widest near middle, sides markedly curved, convergent to narrow apex; sides slightly curved in posterior half, side distinctly sinuate anterior to hind angle; latter obtuse, distinct emargination between hind angle and basal knob; latter small, depressed, pollinose; paramedian grooves deep, pollinose, width at middle more than half that of outer carina; anterior ends of inner carinae pollinose, so the glabrous areas of these carinae appear strongly abbreviated anteriorly; marginal grooves broad; marginal setae absent; angular seta present; prosternum with shallow transverse groove between precoxal carinae; latter not extended to anterior margin of prosternum.

Elytra broad, slightly flattened; humeral tubercles slightly exerted; striae deep, pollinose; intervals narrow, convex, outer ones subcarinate; striole punctures coarse, each puncture about 0.5 as wide as one interval; Stria II with one basal and one apical seta; Stria IV with about six setae; striole without setae; several setae in apex of Stria VII; abdominal Sterna III-V each with coarsely punctate transverse sulcus, in most specimens interrupted at midline; femora with pollinose bands; serrulation of middle tibia less developed than in other members of subgenus; hind calcar of male acute.

The genitalia were figured (Part I, 57; Fig. 26).

This species, from the base of the Cape York Peninsula, is the only known representative of the subgenus in Australia. The subcarinate elytral intervals and unspecialized head put it in Group I. The short, rather broad pronotum separates it from other members of the group.

Kaveinga (sensu stricto) fibulata new species

(Fig. 23)

Type material. — HOLOTYPE male, labelled: "NEW BRITAIN: Rabaul, 29-X, 1940, J.L. Froggatt, in dead stump, C-2408, pres. by Imp. Inst. Ent., BM 1946-35" (BMNH).

Description. — Length 4.8 mm. Antennal Segment I pollinose dorsally; Segments II-V each with narrow dorsal pollinose band; basal setae sparse on Segment VI, well developed on Segments VII-X; head longer than wide; clypeus with margins pollinose with small central glabrous area widely separated from median lobe by pollinose depression; parafrontal boss large, oval, longer than wide, widely separated from median lobe; sides of median lobe broadly sinuate; orbital groove dilated, not extended to posterior margin of eye; temporal lobes slightly longer than wide, their anteromedial margins oblique, convergent posteriorly; medial angle rounded, not overlapped by median lobe; one temporal seta; postorbit entirely pollinose; temporal lobe without overhang in lateral view; suborbital tubercle and gular ridge absent.

Pronotum rather narrow, elongate, length/greatest width 1.20; widest near middle, sides strongly curved to apex and to base; latter only slightly wider than apex; sides not at all sinuate anterior to hind angles; latter rounded; margin not at all sinuate posteromedial to hind angles; paramedian grooves deep, pollinose, broad, at middle nearly equal to outer carinae; anterior ends of inner carinae pollinose, glabrous areas apparently abbreviated anteriorly; marginal groove rather narrow; marginal setae absent; angular seta present; no transverse groove or punctures between precoxal carinae; latter not extended to anterior margin of prosternum.

Elytra narrow, cylindrical; humeral tubercles not exerted; striae deep, pollinose; intervals narrow, convex; outer intervals carinate; stria punctures large, each about 0.33 as wide as an interval; Stria II with one basal and two subapical setae; Stria IV with five setae; Striole without a seta; Stria VII with several setae in apex; abdominal Sterna III-V each with transverse sulcus, latter not interrupted medially; femora with pollinose bands; hind calcar of male small, acute.

Adults are small and narrow, belonging to Group I, but differing from other members of the group in having the hind angles rounded. The members of the *pignoris* complex differ in having the hind angles distinct and the parafrontal bosses markedly reduced or absent. *K. parva*, of Group II, is superficially similar, but has shallow striae which are not continuously pollinose, and has the clypeus continuous with the median lobe.

The *pignoris* complex

The subgenus *Kaveinga (sensu stricto)* is known from three of the Solomon Islands and one island of the Santa Cruz group. Although these beetles are very similar to one another, they do not seem, on the basis of very limited material, to be identical. These four forms could be treated as subspecies of a single species. Since Rhysodini from continental landmasses rarely, if ever, have morphologically distinct subspecies, we prefer to regard the Solomon Island's forms as distinct species. It is nevertheless convenient to describe the complex as a whole before describing the individual species.

Description. — Length 4.9–6.4 mm. Antennal Segment I pollinose dorsally; Segments II-IV each with narrow pollinose band; basal setae various in development; head longer than wide; clypeus with margins pollinose, with small central area glabrous, latter widely separated from median lobe by pollinose depression; parafrontal boss reduced or absent; orbital groove extended to posterior margin of eye or nearly so, dilated anteriorly, tapered posteriorly; temporal lobes as wide as long, anteromedial margin of temporal lobe curved, margins convergent posteriorly; median angle rounded, scarcely overlapped by median lobe; one temporal seta in most specimens (holotype of *K. pignoris* with three temporal setae on one temporal lobe and one on the other); postorbit entirely pollinose; temporal lobe without overhang in lateral view; suborbital tubercle and gular ridge absent.

Pronotum elongate, narrow; hind angles distinct, obtuse; margin distinct posteromedial to hind angle; paramedian grooves deep, pollinose, almost as wide as outer carina at middle of length; anterior end of inner carina pollinose, glabrous part of inner carina apparently abbreviated anteriorly; marginal groove well developed; marginal setae absent; angular seta present; no pits or grooves between precoxal carinae.

Elytra narrow, cylindrical; humeral tubercle not exerted; striae deep, pollinose; intervals narrow, convex, outer ones carinate; stria punctures large; Stria II with setae confined to apex or to base and apex; Stria IV with continuous series of approximately six setae; apical stria without setae; several setae in apex of Stria VII; abdominal Sterna III-VI each with complete transverse sulcus; femora with pollinose bands.

Members of this complex are small and narrow with carinate elytral intervals. They differ from *K. fibulata* in having the hind angles distinct, and separated from the base by an emargination.

Kaevinga (sensu stricto) pignoris new species
(Fig. 25,28,30)

Type material. — HOLOTYPE male, labelled "SOLOMON ISLANDS, Bougainville (S). Kokure, 690 m., June 13, 1956, E.J. Ford, Jr." (BPBM).

Description. — With the characters of the *pignoris* complex; length 5.0 mm; basal setae sparse on antennal Segment VI, well developed on Segments VII-X (Fig. 28); parafrontal boss entirely absent; sides of median lobe broadly, rather shallowly emarginate; temporal lobe evenly rounded posteriorly; pronotum moderately elongate, length/greatest width 1.20; pronotum widest near middle, sides feebly curved except strongly curved near apex; basal knob absent; stria punctures about 0.33 as wide as an interval; Stria II with one seta at base and two to three near apex; hind calcar small, narrow, its apex truncate, its width about 0.6 of apical width of hind tibia.

This species differs from *K. kukum* in having the pronotum shorter, its sides more curved, in having the temporal lobe evenly rounded posteriorly, and in having the hind calcar longer and more distinctly truncate.

Kaveinga (sensu stricto) kukum new species
(Fig. 24)

Type material. — HOLOTYPE male, labelled; "SOLOMON ISLANDS, Guadalcanal, Kukum; 22/4, 1963, P. Greenslade 5109, B.M. 1966-477" (BMNH). PARATYPE female, same data as holotype (mounted on same pin).

Description. — With the characters of the *pignoris* complex; length 5.2–6.4 mm; basal setae sparse on Antennal Segment VI, well developed on Segments VII-X; parafrontal boss entirely absent; sides of median lobe broadly, rather shallowly emarginate; temporal lobe more distinctly sinuate medial to occipital angles than in *K. pignoris*; pronotum more elongate than in *K. pignoris* length/greatest width 1.30; pronotum with sides nearly parallel and straight except at base and apex; small detached basal knob posterior to outer carina; stria punctures about 0.33 as wide as an interval; Stria II with one seta at base and one or two near apex; hind calcar much smaller and less distinctly truncate than in *K. pignoris*, its width about 0.33 of apical width of tibia.

This species is close to the preceding, but differs in the form of the hind calcar, the more elongate pronotum with parallel sides, and the presence of a basal knob on the outer carina.

The paralectotype shows an anomaly which we have not seen in any other rhysodine: the anterior half of the median groove is absent, so that the two inner carinae fuse anteriorly.

Kaveinga (sensu stricto) ulteria new species
(Fig. 26,31)

Type material. — HOLOTYPE male, labelled: "SOLOMON ISLANDS; Santa Cruz Group; Reef Is. 25/11, 1964, 11813 P. Greenslade BM 1966-477" (BMNH); PARATYPE female, same data as male, mounted on same pin, head and prothorax missing.

Description. — With characters of *pignoris* complex; length 5.0 mm; basal setae on Segments VII-X well developed; parafrontal boss absent; sides of median lobe broadly, rather shallowly emarginate; temporal lobe markedly sinuate medial to occipital angle; pronotum rather elongate; length/greatest width 1.28; pronotum with sides parallel except at base and apex; sides markedly curved and narrowed to apex; pronotum with distinct basal knob posteromedial to base of outer carina; stria punctures very coarse, about 0.5 as wide as an interval; hind calcar more elongate, more narrowly truncate than in *K. pignoris* (Fig. 31).

This species differs from both *K. pignoris* and *K. kukum* in having coarser punctures in the elytral striae. The presence of a basal knob on the pronotum is a similarity to *K. kukum*, but the hind calcars of the two species are quite different.

Kaveinga (sensu stricto) nudicornis new species

(Fig. 27,29)

Type material. – HOLOTYPE sex unknown (hind legs missing); labelled: “SOLOMON IS. Russell Islands; Yandina, in logs, 22-24/11/1967, P.J.M. Greenslade, 13463, log 7, B.M. 1966-477” (BMNH).

Description. – With the characters of the *pignoris* complex; length 4.9 mm; basal setae of Antennal Segments VI-X markedly reduced, represented on each segment by one or two lateral setae only (Fig. 29); parafrontal boss represented by small, oblique glabrous area; sides of median lobe more narrowly and deeply emarginate than in related species, thus median lobe strongly constricted at middle; hind margin of temporal lobe not sinuate medial to occipital angle; pronotum elongate, length/greatest width 1.30; pronotum widest at apical fourth, sides strongly curved from there to apex; sides straight, very slightly convergent from widest point to hind angles; basal knob absent from base of outer carina; stria punctures coarse, each puncture about 0.33 as wide as an interval; Stria II without a seta at base, with two setae near apex.

Reduction of the basal setae of the antennae and the sharp constriction of the median lobe of the head differentiate this species from its relatives.

Kaveinga (sensu stricto) parva (Grouvelle 1895) NEW COMBINATION

(This species was accidentally omitted from Part I, 59)

(Fig. 44)

Rhysodes parvus Grouvelle 1895a: 157.

Type material. – HOLOTYPE female, labelled: “Nouv. Guinée, Baie de Geelvink, Raffray & Maindron- 78” (MNHN). Grouvelle, in his written description, cited “Dorey” as the type locality. Geelfink Bay, now called Teluk Sarera, is located on the north side of the western (Indonesian) part of New Guinea. The data is too imprecise to determine whether this species, like its relatives, is a montane one.

Description. – Length 4.8 mm. Antenna without pollinosity; basal setae well developed on Segments VI-X; head longer than wide; clypeus continuous with median lobe; parafrontal boss large, triangular, widely separated from median lobe; sides of median lobe broadly sinuate, orbital groove fine, not extended to posterior margin of eye; temporal lobe oblique, longer than wide; anteromedial margin oblique, nearly straight; margins converging posteriorly; medial angle rounded, well separated from median lobe; one temporal seta; postorbit finely pollinose; temporal lobe with slight overhang in lateral view; suborbital tubercle and gular ridge absent.

Pronotum elongate, narrow; length/greatest width 1.25; widest anterior to middle; sides markedly curved to apex; sides oblique, nearly straight, slightly convergent from widest point to hind angles; latter obtuse; margin shallowly sinuate posteromedial to hind angle; paramedian groove deep, broad, pollinose, at middle nearly equal to outer carinae; inner carinae not at all abbreviated anteriorly, glabrous areas extended anteriorly as far as outer carinae extended; marginal groove deep; marginal setae absent; angular seta present.

Elytra narrow, cylindrical; humeral tubercles not exerted; striae shallow, not pollinose, intervals nearly flat; each stria puncture about 0.25 as wide as an interval, punctures thus coarser than in other members of Group II; Stria II with one basal and one apical seta; Stria IV with seven setae; striole without setae; several setae near tip of Stria VII.

This is a small, narrow species, superficially like *K. fibulata* and the *K. pignoris* complex, but with the clypeus continuous with the median lobe and the elytral striae not continuously pollinose. It differs from the other species from New Guinea in having the pronotum elongate and narrow.

Kaveinga (sensu stricto) cylindrica (Arrow)

(Fig. 32–35)

Rhysodes cylindricus Arrow, 1942: 178.

Type material. – LECTOTYPE male, labelled “PAPUA: Mt. Tafa, 8,500 ft., III-1934, L.E. Cheesman, BM 1934-244” (BMNH). Six PARALECTOTYPES, one male, one female, same data as lectotype; two males, two females, same data as lectotype II-1934 (all (BMNH)).

Description. — Length 5.5–7.0 mm. Antennal Segment I pollinose dorsally; more distal segments not pollinose; basal setae well developed on Segments VI–X; head slightly longer than wide; clypeus with pollinose margins and isolated central glabrous area, latter separated from median lobe by slightly depressed pollinose area; parafrontal boss twice as long as wide, broadly separated from median lobe; median lobe broad, sides of median lobe shallowly sinuate; orbital groove narrow, not quite as long as eye; temporal lobe oblique, wider than long, its anteromedial margin oblique, lobes convergent posteriorly; medial angle rounded, slightly overlapped by median lobe; one to two temporal setae; occipital angles prominent; postorbit glabrous; temporal lobe without overhang in lateral view; gular ridge and suborbital tubercle absent; postorbital tubercle very small or indistinct.

Pronotum as long as wide or slightly longer than wide; pronotum widest near middle, sides slightly curved both anteriorly and posteriorly, sides strongly curved medially near apex; margin sinuate anterior to rectangular hind angle, margin distinctly sinuate posteromedial to hind angle; paramedian grooves deep, pollinose, strongly narrowed in middle, less than 0.33 as wide as outer carina at middle; anterior ends of inner carinae pollinose, so that glabrous areas appear abbreviated anteriorly; posterior end of outer carina depressed, pollinose; basal knob of outer carina pollinose; marginal groove rather narrow; one to three marginal setae present; angular seta present; precoxal carinae reaching anterior margin of prosternum; a transverse groove present between precoxal carinae.

Elytra narrow, cylindrical; humeral tubercle narrow, not exerted (Fig. 35); Striae I, II slightly impressed; remaining striae represented by rows of punctures; intervals flat; stria punctures small, less than 0.2 times as wide as one interval; Stria II with one basal seta, without apical seta; Stria IV with four to five setae; Striole without setae; Stria VII with several setae near apex; abdominal Sterna III–V each with uniseriate transverse row of punctures, latter not interrupted at midline; anterior femora with fine pollinose bands, other femora with pollinosity reduced or absent; hind calcar of male small, rather obtuse.

This species is broader and has a shorter pronotum than does *K. parva*, and is narrower and more cylindrical than are the remaining members of Group II. The most similar species is *K. lupata*, which has broader elytra with the humeral tubercle strongly exerted.

Range. — *K. cylindrica* is confined to the most eastern mountains of New Guinea, from Mt. Tafa to the vicinity of Wau. In addition to the type material, we have seen the following specimens: one male, 6 km W of Wau, Nami Creek, 1700 m, 10-VI-1962, coll. J. Sedlacek; one male, Mt. Missim, 1500–2000., 22-30-IV-1968, coll. J.L. Gressitt, R.C.A. Rice & J. Sedlacek; one female, Mt. Kaindi, 2250 m., 10-V-1968, coll. J.L. Gressitt, J. Sedlacek (all BPBM).

Kaveinga (sensu stricto) lupata new species
(Fig. 36–39)

Type material. — HOLOTYPE male, labelled; “New Guinea: (NE) Mt. Kaindi, 16 km SW of Wau, 2300 m., 8-9-VI-1962, coll. J. Sedlacek” (BPBM). 17 PARATYPES (all BPBM); five males, same data as holotype; one female, same locality and collector as holotype, 10-I-1962, one male, two females, “N. Guinea (NE) Wau, 2400 m., 9-12-I, 1962, coll. J. Sedlacek, C. Monteith & native”; two males, “N. Guinea (NE) Wau, Morobe Dist. 2400 m., 9-12-I-1962, coll. J.H. & M. Sedlacek C. Monteith & native”; one male, “N. Guinea (NE) Wau, Morobe Dist. 1300 m., 28-I-1963, coll. J. Sedlacek”; one female, “N. Guinea (NE) Wau, Morobe Dist., 1700–1800 m., 7-X-1962, coll. J. & M. Sedlacek”; one male, “N. Guinea (NE) 6 km W of Wau, Nami, Creek, 1700 m., 10-VI-1962, coll. J. Sedlacek”; one female, same locality, collector, 12-VI-1962; one female, “N. Guinea (NE) Wau, Morobe Dist., Nami Creek, 1600–1650 m., 24-II-1963, coll. J. Sedlacek”; one male, “N. Guinea (NE), Ialibu, 2900 m., 8-14-1968, coll. Gressitt & Maa”.

Description. — Length 5.0–6.2 mm. Antennal Segment I pollinose dorsally, more distal segments not pollinose; basal setae sparse on Segment VI, well developed on Segments VII–X; head slightly longer than wide; clypeus with pollinose margins, and glabrous central area; latter narrowly separated from median lobe by shallow pollinose depression in some specimens, clypeus and median lobe narrowly joined at midline in other specimens; parafrontal boss twice as long as wide, broadly separated from median lobe; median lobe broad, sides of median lobe shallowly sinuate; orbital groove slightly dilated, ended opposite middle of eye; temporal lobe oblique, slightly wider than long, its anteromedial margin oblique; the two lobes convergent posteriorly; medial angle rounded, slightly overlapped by median lobe; one temporal seta inserted in enlarged puncture; temporal lobe deeper than that of *K. cylindrica*, distinctly overhanging occiput in lateral view; distinct gular ridge lateral to each gular groove; each ridge ended posteriorly in prominent suborbital tubercle (Fig. 39); postorbital tubercle absent.

Pronotum as wide as long, widest near base, sides almost parallel except strongly convergent near anterior margin; margin not sinuate anterior to hind angle, latter rectangular; margin scarcely emarginate posteromedial to hind angle; paramedian grooves deep, entire, moderately wide, about 0.5 as wide as outer carina at middle; anterior ends of inner carinae pollinose, so that glabrous areas appear abbreviated anteriorly; posterior end of outer carina depressed, pollinose; basal knob of outer carina pollinose; marginal groove narrow; marginal setae absent from most specimens, a few specimens with one marginal seta anterior to the angular seta; precoxal

carinae not extended to anterior margin of prosternum; transverse row of two pits between precoxal carinae.

Elytra somewhat flattened, broader than in *K. cylindrica*; humeral tubercle prominently exerted (Fig. 36); elytral striae not impressed, represented only by rows of punctures; intervals flat; stria punctures small, less than 0.2 of width of one interval; Stria II with one basal seta, and in most specimens with one apical seta; in some specimens apical seta absent from Stria II, but apical seta in Stria I; Stria IV with four to five setae; Striole without a seta; Stria VII with five to ten setae near apex; abdominal sterna III-V each with uniseriate transverse row of punctures, the row not interrupted in midline; anterior femora with fine pollinose bands; remaining femora without pollinosity; hind calcar of male very small.

This species is sympatric with *K. cylindrica*, but is readily separated by the exerted humeral tubercles, the wider paramedian and marginal grooves, and the well-developed gular ridges and suborbital tubercles.

With this species we provisionally place one specimen from Mt. Missim, New Guinea, 1650 m (BPBM). It matches the description of *K. lupata* in most respects, but differs in having the suborbital tubercles almost absent; the parafrontal bosses large, quadrate, and the total length 6.8 mm. Since we have doubts about the inclusion of this species, we have not designated it as a paratype.

Kaveinga (sensu stricto) okapa new species
(Fig. 40)

Type material. – HOLOTYPE male, labelled: "New Guinea; Okapa, Kamira, Eastern Highlands, 2-9-1964, coll. R. Hornabrook (NMNZ). Seven PARATYPES (NEW GUINEA) one female, same data as holotype; one male, Okapa, 12-11-1964; one female, Okapa, Okosa, 12-1-1965; one female, Daulo Pass, Asato-Chimbu Divide, 8-4-1972 and one male, 16-9-72; one female, 18-10-72 and one male, Feb., 1971, Lufa, Mt. Michael. All specimens collected by R. Hornabrook and deposited at NMNZ.

Description. – Length 5.0–6.3 mm. Antennal Segment I pollinose dorsally, more distal segments not pollinose; basal setae sparse on Segment VI, well developed on Segments VII-X; head slightly longer than wide; clypeus with pollinose margins, glabrous central area; latter narrowly separated from median lobe by shallow pollinose depression in some specimens, clypeus and median lobe narrowly joined at midline in other specimens; parafrontal boss connected narrowly to median lobe; median lobe broad, its lateral margins nearly parallel; orbital groove slightly dilated, short, ended well anterior to posterior margin of eye; temporal lobe oblique, slightly longer than wide, its anteromedial margin oblique; lobes convergent posteriorly; median angle rounded, slightly overlapped by median lobe; one temporal seta, inserted in prominent puncture; occipital angle prominent, somewhat lobate; postorbit extensively glabrous; pollinosity not extended to eye; temporal lobe with slight overhang in lateral view; gular ridge prominent, partly to entirely pollinose; posterior end of gular ridge in form of prominent suborbital tubercle.

Pronotum varied in size and proportions, in most specimens as wide as long, greatest width at base; in few specimens slightly longer than wide, with widest point near middle, and base slightly narrowed; lateral margin not sinuate anterior to hind angles, latter rectangular; paramedian grooves deep, markedly narrowed at middle, their outer margins straight, elevated, sharply defined; their inner margins ill-defined, sloped gradually from inner carinae; pollinosity of paramedian groove reduced to narrow strip along outer margin; anterior end of inner carina pollinose, inner carina apparently abbreviated anteriorly; basal knob pollinose, depressed below level of outer carina; marginal groove fine; marginal setae absent; angular seta present; precoxal carinae ending close to anterior margin of prosternum; a transverse row of two pits between precoxal carinae.

Elytra broad, slightly flattened; humeral tubercle slightly exerted; elytral striae not at all impressed, represented only by rows of fine punctures; intervals flat; stria punctures small, less than 0.2 as wide as an interval; Stria II with basal seta and apical seta or one or both of these absent; Stria IV with one or two setae near base and one at apex, but without setae in middle third; Striole asetose; Stria VII with seven to ten setae near apex; abdominal Sterna III-V each with uninterrupted transverse row of punctures; femora with pollinose bands absent or represented by small vestiges; hind calcar of male very short, obtuse.

This species and *K. marifuanga* differ from all other members of the subgenus in having the parafrontal bosses joined to the median lobe. This species is distinguished by having large suborbital tubercles, parafrontal bosses only narrowly joined to the median lobe, and the latter, at most narrowly in contact with the clypeus. In most specimens of *K. okapa*, the pronotum is much less elongate than in *K. marifuanga*, and is not at all narrowed at the base. In a few specimens, which we provisionally interpret as variants of *K. Okapa*, the pronotum is slightly elongate and slightly narrowed at the base, approaching that of *K. marifuanga*. Possibly we are including more than one species in our concept of *K. okapa*. The point cannot be settled until many more specimens are available.

Kaveinga (sensu stricto) marifuanga new species

(Fig. 41, 42)

Type material. – HOLOTYPE male, labelled: "NEW GUINEA, Marifuanga, Asaro-Chimbu Divide, 1-6-72, coll. R. Hornabrook" (NMNZ). Three PARATYPES: one male, same data as holotype; two females, Daulo Pass, Asato-Chimbu Divide, 8-4-72 and 4-1-75, coll. R. Hornabrook (all NMNZ).

Description. – Length 5.4–7.0 mm. Antennal Segment I pollinose dorsally, more distal segments not pollinose; basal setae sparse on Segment VI, well developed on Segments VII–X; head slightly longer than wide, clypeus with pollinose anterior and lateral margins, broadly joined to median lobe posteriorly; parafrontal boss broadly fused to median lobe; median lobe broad, its lateral margins nearly parallel; orbital groove slightly dilated, short, ending anterior to middle of eye; temporal lobe oblique, slightly longer than wide, its anteromedial margin oblique, straight; temporal lobes convergent posteriorly; medial angle rounded, slightly overlapped by median lobe; one temporal seta, inserted in prominent puncture; occipital angle prominent, in form of small lobe; postorbit glabrous; temporal lobe not overhanging occiput in lateral view; gular ridge low, glabrous, its posterior end in form of small suborbital tubercle (suborbital tubercles smaller and closer together than in *K. okapa*). Pronotum distinctly longer than wide, length/greatest width averages 1.16; widest near middle, sides curved to apex, nearly straight, slightly convergent posteriorly; margin distinctly sinuate anterior to hind angles; latter rectangular; paramedian grooves shallower than in *K. okapa*, markedly narrowed at middle, their outer margins straight, elevated, sharply defined; their inner margins ill-defined, sloped gradually from inner carinae; pollinosity of paramedian groove reduced to narrow strip along outer margin; anterior end of inner carina not pollinose nor apparently abbreviated; basal knob of outer carina glabrous, appearing as continuation of outer carina; marginal groove fine; marginal setae absent from most specimens, but one present unilaterally near anterior angle on one specimen; angular seta present; prosternum with two pits in transverse row between precoxal carinae.

Elytra relatively narrow, cylindrical; humeral tubercles not exerted; elytral striae not impressed, represented by rows of punctures; intervals flat; stria punctures very small, less than 0.15 as wide as an interval; Stria I in some specimens with seta near apex, in other specimens this seta absent; Stria II without setae; Stria IV with one seta near base and two near apex; Striole without setae; Stria VII with approximately nine setae near apex; Sternites III–V each with transverse row of coarse punctures, latter broadly interrupted in midline; femora with pollinose bands absent; hind calcar obtuse, but more prominent than in *K. okapa*.

This species is similar to *K. okapa*, but differs in having the suborbital tubercles much smaller, the clypeus broadly joined to the median lobe; the parafrontal bosses more broadly joined to the median lobe, and the transverse rows of punctures of the abdomen broadly interrupted in the midline. The pronotum is very different in shape from most specimens of *K. okapa*, but a few specimens which we interpret as variants of the latter species approach the shape seen in *K. marifuanga*.

Kaveinga (sensu stricto) occipitalis (Grouvelle 1903)

(Fig. 43)

Rhysodes occipitalis Grouvelle 1903: 105–106.

Type material. – HOLOTYPE female, labelled; "NUOVA GUINEA, Fly River, L.M. D'Alberty 1876-1877" (MNHN).

Description. – Length 7.0 mm. Basal setae sparse on Segment VI, well developed on Segments VII–X; head distinctly wider than long; clypeus with glabrous central area, narrow pollinose anterior margin and widely pollinose lateral margins, separated from median lobe by deep pollinose transverse impression; clypeus not constricted posteriorly; median lobe connected to each antennal rim by oblique, pollinose carina, but true parafrontal bosses absent; sides of median lobe shallowly sinuate; orbital groove very broadly dilated, extended beyond posterior margin of eye; temporal lobe transverse, its anterior margin rounded, its medial angle closely fitted to and overlapped by median lobe; median and temporal lobes not rugose; posterior margin of temporal lobe transverse, its most posterior point midway between midline and lateral margin of head; one temporal seta, inserted in prominent puncture; postorbit pollinose; temporal lobe without overhang in lateral view; gular ridge and suborbital tubercle absent.

Pronotum as wide as long, widest at base; sides nearly straight, slightly convergent almost to apex, where they are strongly curved medially, lateral margin not sinuate anterior to hind angle; latter rectangular; anterior margin of pronotum deeply emarginate medially; paramedian grooves deep, rather markedly narrowed at middle, width at middle about 0.5 width of outer carina; anterior end of inner carina pollinose, latter much shorter than outer one, appearing oval; posterior end of outer carina not depressed; basal knob absent; marginal groove deep, holotype with one marginal seta on left side, just anterior to angular seta, but without marginal seta on right side; angular seta present; precoxal carina not extended to anterior margin of prosternum; no pits or transverse grooves between precoxal carinae.

Elytra broad, somewhat flattened; humeral tubercle exerted; striae deep, pollinose, intervals carinate; Intervals II, III more elevated than others at base, slightly prominent, in form of slight anterior prominence; stria punctures oval, longer than wide, about

0.33 as wide as interval; Stria II with one basal and one apical seta; Stria IV with one basal and two apical setae; apical striole without setae; Stria VII with about ten setae near apex; abdominal Sterna III-V each with complete transverse sulcus; Sternum VI with complete basal transverse sulcus and group of coarse punctures near apex; femora with pollinose bands.

This is the least specialized member of Group III, the "short-faced" species. It differs from the other members of the group in having the temporal lobes transverse posteriorly. The broad head and the deep pollinose elytral striae will separate it from all other known *Kaveinga* species from New Guinea, all of which belong to Group II.

Kaveinga (sensu stricto) histrio new species
(Fig. 45-48)

Type material. – HOLOTYPE male, labelled; "Mindanao, E. Slope Mt. McKinley, 3300 ft., Davao Prov., X-1-46, H. Hoogstraal (CNHM Philippines Zoo. Exped. 1946-57)" (CNHM). Two PARATYPES, one female, same data as type; one female, same locality as type, IX-28-1946, F.G. Werner (both CNHM).

Description. – Length 5.5–7.0 mm. Antennal Segment I pollinose dorsally; Segments II-V each with narrow pollinose band; basal setae well developed on Segments VI-X; head twice as wide as long, much deeper than long; clypeus entirely pollinose, constricted at base, its sides angulate, its anterior and lateral margins raised; clypeus separated from median lobe by deep pollinose impression; anterior tentorial pits enlarged, close together; parafrenal boss absent; median lobe with lateral margins straight; median lobe sloped abruptly from postclypeal depression, markedly convex in lateral view (Fig. 46); posterior end of median lobe curved ventrally over occiput; orbital groove markedly dilated; extended beyond posterior margin of eye; two temporal setae, each inserted in prominent pit, one or both of latter confluent laterally with orbital groove in some specimens; temporal lobe much wider than long, curved, its medial margin closely fitted to median lobe but not countersunk in it or extended above it; median lobe smooth, temporal lobe with few longitudinal rugae near border with median lobe; temporal lobe markedly divergent posteriorly; posterior margin of temporal lobe oblique, sinuate, most posterior point much closer to lateral margin than to midline; postorbit pollinose; temporal lobe without overhang in lateral view; gular ridge, suborbital tubercle absent.

Pronotum slightly longer than wide; length/greatest width 1.1; widest slightly anterior to middle; sides curved; base and apex both narrowed; lateral margin shallowly sinuate anterior to hind angle, latter nearly rectangular; anterior margin of pronotum shallowly emarginate medially; paramedian grooves wide, deep, as wide at middle as are outer carinae; both inner and outer carinae pollinose and apparently abbreviated anteriorly; inner carinae more abbreviated than outer one; basal knob of outer carina glabrous, prominent, separated from rest of carina by pollinose depression; marginal groove broad, deep; one marginal seta near anterior angle (unilaterally absent in one specimen); one to two marginal setae near angular seta; angular seta present; precoxal carinae prominent, but not extended to anterior margin of prosternum; transverse groove between precoxal carinae; anterior part of prosternum and precoxal carinae pollinose; anterior part of pleuron pollinose, pollinosity extending posteriorly along notopleural suture.

Elytra narrow, cylindrical; humeral tubercle pilose at base, not exerted; striae deep, very narrowly pollinose; intervals convex but not carinate; stria punctures very large, about 0.33 as wide as an interval; Stria II with one seta at base and two near apex; Stria IV with four to six setae; striole with one seta; Stria VII with one seta at humerus and six near apex; Sternum II of abdomen with two transverse rows of punctures; Sterna III-V each with complete transverse sulcus; Sternum VI with basal sulcus which is interrupted in midline and with group of coarse punctures near apex; femora with pollinose band; hind calcar of male small, obtuse.

In this species and the next one, the head is an extraordinary, masklike structure, rising high above the pronotum, and largely hollowed posteriorly, exposing the slender pillar which supports the median lobe (Fig. 47). In dorsal view, the diverging temporal lobes suggest the head of the hammer-head shark (*Sphyrna*). The long orbital grooves, the smooth median lobe, and the abbreviated pronotal carinae provide convenient separation of this species from *K. strigiceps*.

Kaveinga (sensu stricto) strigiceps new species
(Fig. 49-51)

Type material. – HOLOTYPE male, labelled; "Buru, Station 12, 4-7 Febr. 1922, L.J. Toxopeus" (AMS).

Description. – Length 5.4 mm. Antennal Segment I pollinose dorsally; Segments II-V each with narrow pollinose band; basal setae well developed on Segments VI-X; head almost twice as wide as long, twice as deep as long; clypeus glabrous in middle, its anterior and lateral margins pollinose; clypeus constricted at base, its anterior margin curved; margins of clypeus reflexed; clypeus

separated from median lobe by deep pollinose depression; anterior tentorial pits greatly enlarged, close together; parafrontal boss absent; median lobe with lateral margins straight; median lobe sloped almost vertically from postclypeal depression, markedly convex in lateral view; posterior end of median lobe curved ventrally over occiput (Fig. 50); anterior half of median lobe longitudinally rugose, posterior half with few scattered rugae, but otherwise smooth; orbital groove dilated, not extended posterior to eye; one temporal seta far from orbital groove; temporal lobes oblique, divergent posteriorly, posterior margin of temporal lobe sinuate; temporal lobe densely, longitudinally rugose (Fig. 51); temporal lobes very convex, sloped above and partly overlapping median lobe; postorbit entirely pollinose, gular ridge, suborbital tubercle absent.

Pronotum as wide as long, nearly quadrate; margins straight and parallel except near apex, where they curve medially; lateral margin not sinuate anterior to hind angle, latter rectangular; anterior margin of pronotum shallowly emarginate medially; paramedian grooves deep, narrower than in *K. histrio*, at middle equal in width to outer carina; neither outer nor inner carina abbreviated or pollinose anteriorly; basal knob of outer carina small, depressed, pollinose; marginal groove deep, broad; marginal setae absent; angular seta present; inner carina with basal seta; precoxal carinae not extended to anterior margin of prosternum; no transverse groove or pits between precoxal carinae; anterior part of prosternum, precoxal carinae, and propleura pollinose; pollinosity of pleuron extended posteriorly along notopleural suture.

Elytra narrow, cylindrical; humeral tubercle not exerted; striae deep, narrowly pollinose; intervals convex, narrow, but not carinate; stria punctures very small, less than 0.2 of width of one interval; Stria II without setae; Stria IV with one apical seta; Striole without seta; Stria VII with few setae near apex; Sternum II of abdomen with two transverse rows of punctures; Sterna III-V each with complete transverse sulcus; Sternum VI with transverse basal sulcus interrupted at midline, and group of coarse punctures near apex; femora with pollinose bands; lateral margin of middle tibia scarcely serrulate; hind calcar of male small, acute.

The high, domed head with conspicuous rugae on both median and temporal lobes easily separate this species from all others.

SUBTRIBE CLINIDIINA

Description. – Part I, 59.

Key to Genera. – Part I, 59

Genus *Grouvellina* Bell and Bell, 1978

(Fig. 52-74)

Type species. – *Rhysodes tubriceps* Fairmaire 1868.

Description. – Antennal stylet well developed; antennal segments with both basal and apical series of setae well developed; minor setae of antennal segments forming a ventral tuft on each segment, in most species beginning on Segment V; dorsal side of antennal segments with bands or spots of pollinosity.

Eye large, deeper than long, with about 150 ommatidia; antennal lobe separated from temporal lobe by deep postantennal groove; most species with elevated glabrous parafrontal boss lateral to median lobe and anterior to postantennal groove; head extensively pilose, in most species with well-developed orbital band of pilosity in place of orbital groove; longer pilosity in frontal pit; pilosity of occipital region in form of "ruff" anterior to glabrous neck condyle; labrum with one or two pairs of setae; clypeus with one pair; two to six temporal setae; postlabials one to many pairs.

Pronotum with complete paramedian grooves; marginal groove single, complete in most species (but abbreviated posteriorly in *G. grouvellei*); prothorax with "collar" of long pilosity around the anterior margin; angular seta present; 0 to six marginal setae.

Elytral striation complete; Stria VII marginal; apical striae absent; pilosity well developed in elytral striae (in some species also invading intervals); hind wings well developed in those species checked. Abdominal sterna transversely sulcate.

Anterior tibia with cleaning organ entirely or largely distad to base of tarsus; middle of cleaning organ with short, stiff spinose setae, in form of "comb", in most species sharply contrasted with longer, flexible setae at either end of the row, in form of pair of "brushes"; in most species both proximal and distal spurs distinct, opposite the "brushes" (in a few species, proximal spur absent); distal spur apparently secondary point on preapical tooth; proximal spur inserted just distad of intermediate tooth.

Apex of middle tibia alike in both sexes, with one spur and a medial process (in some species also with a lateral process); male without middle calcar; hind tibia in female with two spurs; in male with one spur and a calcar; all legs with a complex pattern of pilose and glabrous areas.

The genus is unique among Clinidiina in possessing large eyes, functional hind wings, and complete elytral striation. *Grouvellina* is known only from Madagascar, but *Rhysodes planifrons* Fairmaire 1893, described from Mayotte, in the Comoro Islands, will probably prove to belong to the genus. We have

been unable to locate the type of this species or that of *Rhysodes canaliculatus* Castelnau 1836. The description of the latter species is consistent with membership in *Grouvellina*, but is not detailed enough to indicate to which, if any, of the species described below it applies. The size range is consistent with it being *G. hova*, *G. cuneata*, or *G. gigas*.

Phylogeny. – The radiation of this remarkable genus must have taken place entirely within Madagascar. Deciphering the phylogeny has proven difficult, as many of the characters occur in bewildering combinations. It is not made easier by the fact that six of the species are known from one sex only, that four species are not known from any specific locality, and that six of the remaining species are recorded from one locality each. The above figures suggest that we know only a fraction of the actual species.

We present a hypothetical phylogenetic diagram of the genus (Diagram 1). Species 1, the hypothetical common ancestor of the genus, is presumed to have had the following characteristics: antenna with tufts of minor setae on Segments V-X; antennal Segments II-X each with complete dorsal apical and basal bands of pollinosity; head slightly longer than broad; labrum with two pairs of setae; median lobe glabrous; parafrontal boss present; orbital groove represented by a complete band of pollinosity medial to the eye; all pronotal carinae extended the full length of the pronotum, and broadly glabrous; all pronotal grooves complete and deep; pronotum with several marginal setae; precoxal carina well developed; elytral intervals equal, subcarinate; Stria I with several setae near the apex; Striae II and IV with complete series of setae; metasternum coarsely punctate on disc and margins; anterior femur with a ventral tooth in both sexes; anterior tibia of male with proximal tooth (absent in female).

Of these characters, perhaps the most important are the number of setae on the labrum, the presence of the ventral femoral and proximal tibial teeth, and the precoxal carina. Four is the number of labral setae in the more primitive genera of Rhysodini, and it is closer to the number characteristics of most other Carabidae (six), therefore it is reasonable to conclude that having only two setae is a derived characteristic. Femoral and proximal tibial teeth are present in a number of otherwise very dissimilar *Grouvellina*; therefore it seems likely that they were present in the common ancestor, and have been lost independently several times. The same line of reasoning leads us to hypothesize the presence of the precoxal carina in Species 1. *Grouvellina tubriceps* is the one member of this genus which has all the hypothetical ancestral characteristics.

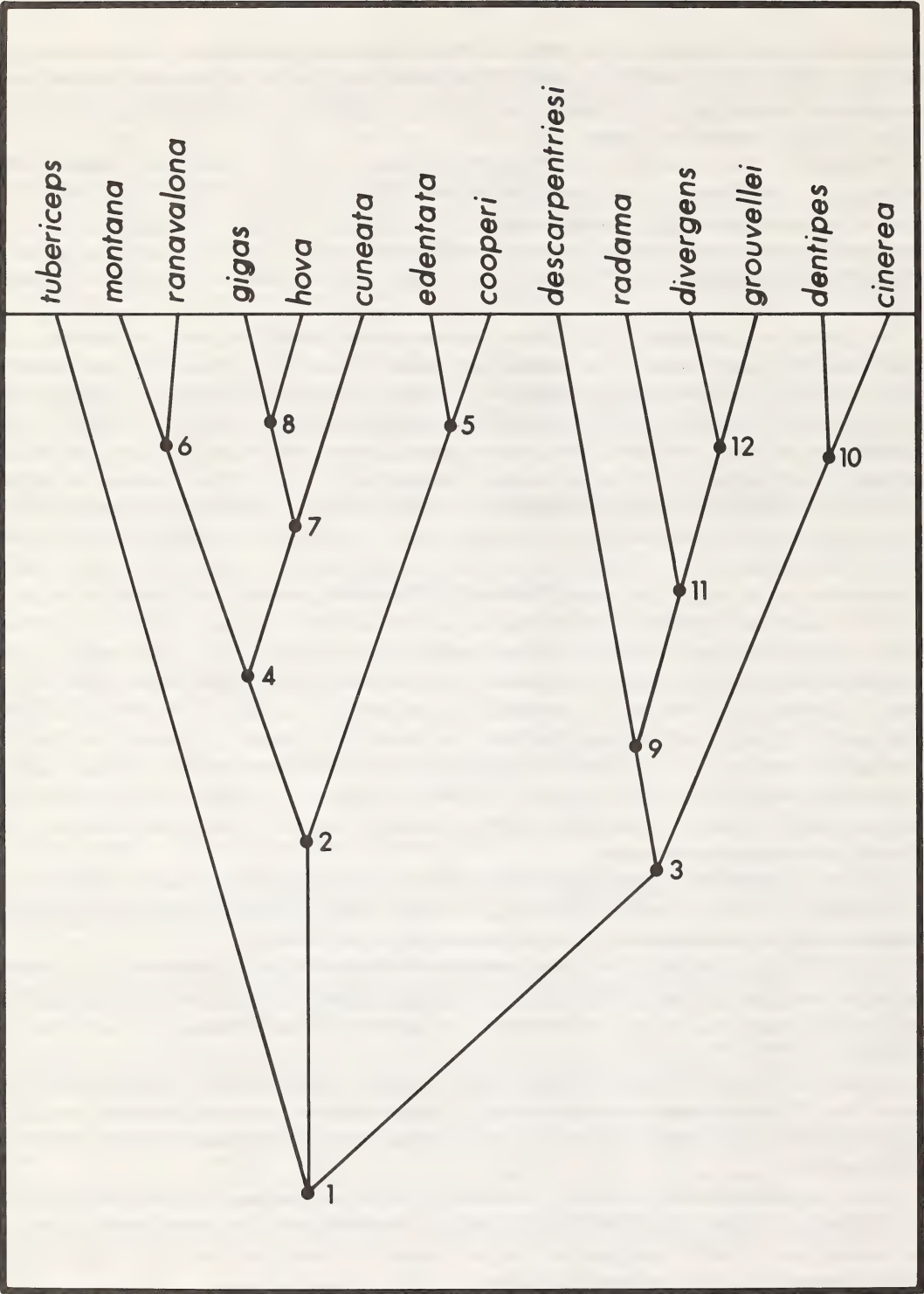
With the exception of *G. tubriceps*, all *Grouvellina* can be assigned to two major lines, descended respectively from Species 2 and 3. In Species 2, the basal bands of pollinosity were lost from antennal Segments III-X; while in Species 3, the lateral setae of the labrum were lost.

Species 2 was the ancestor of two lines, represented by Species 4 and 5. Species 4 lost the precoxal carina but was otherwise not modified. Species 5 retained the precoxal carina, but lost the femoral and proximal tibial teeth, and the basal pollinose band on Segment II of the antennae, and the anterior setae of Stria II.

Species 5 was the ancestor of *G. edentata* and *G. cooperi*. *G. edentata* lost the anterior setae from elytral Stria II, but otherwise remain unmodified. *G. cooperi* retained one anterior setae in Stria II, but had the posterior setae of that stria reduced to one, and lost the parafrontal boss and the marginal setae of the pronotum.

Species 4 gave rise to Species 6 and 7. In Species 6, the metasternal punctures were reduced in size and the anterior setae of Stria II were lost. In Species 7, the metasternal punctures remained large and the anterior setae in Stria II remained, but the head became short and broad, the body increased in size, and the intervals became more distinctly carinate.

Species 6 is the ancestor of *G. montana* and *G. ranavalona*. The former species lost the anterior part of the orbital pilose band, while the metasternal (discal) punctures disappeared entirely, the marginal



Phylogenetic Diagram I. Reconstructed Phylogeny of species of *Grouvellina*.

setae of the pronotum were reduced in number, the body size diminished, and the elytra intervals became flattened. The femoral and proximal tibial teeth were retained. In *G. ranavalona* the femoral tooth was lost, while the size remained large and the metasternal punctures remained distinct, though fine. The male of this species is unknown, but it seems likely that it will be shown to lack the proximal tibial tooth. (All of the known males of *Grouvellina* which do not have a femoral tooth lack the proximal tibial tooth as well.)

Species 7 was the ancestor of Species 8 and of *G. cuneata*. In Species 8, Stria I lost its setae, while in *G. cuneata* these setae were retained, but the anterior setae of Stria II were lost, the pronotum became strongly narrowed anteriorly, and the striae and intervals became strongly unequal.

The two descendants of Species 8 are *G. gigas* and *G. hova*. The former species remains essentially like Species 8, while the latter species lost the parafrontal boss.

Species 3 (the common ancestor to the species with two labral setae) was ancestral to Species 9 and Species 10. In Species 9, the basal pollinose bands of the outer antennal segments became broken into isolated pilose spots, and the femoral and proximal tibial teeth were lost. Species 10 retained the pollinose bands intact, and retained the femoral and proximal tibial teeth, but became highly specialized in many features, including the abbreviation of the outer pronotal carina posteriorly, the development of pollinosity on the median lobe, the loss of all but the most anterior of the pronotal marginal setae, and the loss of the parafrontal boss. In addition, the head became shortened and conspicuous tufts of pollinosity developed around each temporal seta.

Species 9 gave rise to *G. descarpentriesi* and to Species 11. The former species lost the discal punctures of the metasternum, the precoxal carina, the setae of Stria I and the setae of the anterior half of Stria II. The apical pollinose rings of the outer remained intact. Species 11 had the apical band broken into isolated pilose spots, but it retained the metasternal punctures, the precoxal carinae and the setae of Stria I and the anterior half of Stria II.

Species 11 gave rise to *G. radama* and Species 12. *G. radama* remained close to Species 11 in structure, but the median lobe became very narrow and the postlabial setae underwent multiplication. Species 12 lost the tuft of minor setae and the basal setae from antennal Segment V, while the marginal carina became abbreviated posteriorly, the precoxal carina was lost and the metasternal punctures became fine.

Species 12 gave rise to *G. divergens* and *G. grouvellei*. The former species remains close to Species 12 in structure, but has lost the marginal setae of the pronotum and the anterior setae from Stria II. *G. grouvellei* retains these setae, while it has become highly specialized in having the pollinosity greatly increased so that it covers almost the entire dorsal surface, while the pronotal carinae and elytral intervals have become much less convex.

Species 10 gave rise to *G. dentipes* and *G. cinerea*. *G. dentipes* retained the femoral and proximal tibial teeth, while *G. cinerea* lost them.

The above phylogeny is by necessity somewhat speculative, and doubtless will require some modification when more is known about *Grouvellina*. Perhaps the most questionable points are the existence of Species 6 (a common ancestor for *G. montana* and *G. ranavalona*), and the question of whether *G. radama* is really more closely related to Species 12 than is *G. descarpentriesi*.

KEY TO SPECIES

- | | | |
|---|--|---|
| 1 | Outer carina of pronotum complete, glabrous, extended from anterior margin to vicinity of hind angle; marginal carina glabrous, ended distinctly anterior to hind angle..... | 2 |
|---|--|---|

1'	Outer carina not both complete and glabrous, either abbreviated clearly anterior to hind angle or else entirely pollinose and coalescent with marginal carina posteriorly	12
2 (1)	Femur of anterior leg with ventral tooth in both sexes; male with proximal tooth on anterior tibia (Fig. 74)	3
2'	Femur of anterior leg without ventral tooth; male (where known) without proximal tooth on anterior tibia	7
3 (2)	Orbital groove complete, pilose, eye and temporal lobe separated; elytral intervals more or less carinate	4
3'	Orbital groove incomplete, eye in contact with glabrous area of temporal lobe; elytral intervals not carinate	<i>Grouvellina montana</i> new species, p. 419
4 (3)	Head with large distinct parafrontal boss	5
4'	Parafrontal boss absent, entire superantennal area pollinose or pilose	<i>Grouvellina hova</i> new species, p. 417
5 (4)	Lateral margins of pronotum markedly convergent anteriorly, width at middle less than width at base; inner striae narrower than outer ones	<i>Grouvellina cuneata</i> new species, p. 416
5'	Lateral margins of pronotum not markedly convergent, width at middle equal to or greater than width at base; inner and outer striae of equal width	6
6 (5')	Prosternum with short precoxal carina; body length 6.0–8.0 mm; postmentum glabrous (Fig. 60); dorsal basal pollinose bands on antennal Segments II–VIII (Fig. 59); median lobe long, narrow	<i>Grouvellina tubriceps</i> (Fairmaire), p. 413
6'	Precoxal carina absent; body length 8.0–10.5 mm; postmentum pollinose (Fig. 63); dorsal basal pollinose bands only on antennal Segment II (Fig. 62); median lobe short, broad, broadly rounded posteriorly	<i>Grouvellina gigas</i> new species, p. 413
7 (2')	Labrum with four setae	8
7'	Labrum with two setae	10
8 (7)	Precoxal carina absent; elytral intervals carinate; base of elytral interval II not elevated; length 9.0 mm or more	<i>Grouvellina ranavalona</i> new species, p. 417
8'	Precoxal carina present; elytral intervals not carinate; base of elytral interval II elevated; length 5.0–7.0 mm	9
9 (8')	Parafrontal boss present	<i>Grouvellina edentata</i> new species, p. 418
9'	Parafrontal boss absent	<i>Grouvellina cooperi</i> new species, p. 418
10 (7')	Median lobe of head long, narrow, parallel-sided; carinae of pronotum narrow, equal to or slightly wider than pronotal grooves; precoxal carina present	<i>Grouvellina radama</i> new species, p. 419
10'	Median lobe of head wider; carinae of pronotum wider than pronotal grooves; precoxal carina absent	11
11 (10')	Medial angle of temporal lobe rounded; antennal stylet elongate, acute; discal metasternal punctures absent; pronotum with 4–5 marginal	<i>Grouvellina descarpentriesi</i> new species, p. 420
11'	Medial angle of temporal lobe more pointed; antennal stylet obtuse; discal metasternal punctures present; marginal setae absent	<i>Grouvellina divergens</i> new species, p. 421
12 (1')	Outer carina of pronotum entirely glabrous, abbreviated posteriorly; marginal groove of pronotum complete; each temporal seta concealed within dense tuft of pilosity, temporal lobe otherwise glabrous	13
12'	Outer carina completely pollinose or with small glabrous areas; outer carina not	

- abbreviated posteriorly, but coalescent with marginal carina, marginal groove incomplete; temporal lobe largely pilose, no tufts around setae *Grouvellina grouvellei* (Fairmaire), p. 421
- 13 (12) Medial angle of temporal lobe more distinct; anterior femur with ventral tooth; male with proximal tooth on anterior tibia *Grouvellina dentipes* new species, p. 422
- 13' Medial angle of temporal lobe more rounded; anterior femur without ventral tooth; male without proximal tooth on anterior tibia *Grouvellina cinerea* new species, p. 423

Grouvellina tubriceps (Fairmaire, 1868)
(Fig. 58-60)

Rhysodes tubriceps Fairmaire, 1868: 782.

Type material. – HOLOTYPE male, labelled; “Madagascar” (MNHN); labelled as Fairmaire type. According to the original description, the specimen was collected by Charles Coquerel. The holotype is in poor condition with hind legs missing and perhaps some setae broken off.

Description. – Length 6.0–8.0 mm. Antennal Segment XI as long as wide; apical stylet short, conical; tufts of minor setae on Segments V–X; antennal Segment I extensively pollinose on dorsal aspect; Segments II–IX each with two transverse pollinose bands; Segment X with basal band only (Fig. 59). Head slightly elongate; frontal and postantennal grooves deep, relatively wide; median lobe relatively narrow, obtusely pointed posteriorly; parafrontal bosses well developed; temporal lobe slightly longer than wide; sinuate anterior to medial angles, latter narrowly separated, obtusely pointed; two to three temporal setae; four labral setae; orbital groove complete, broadly pilose; three to four pairs of postlabial setae; mentum pollinose, postmentum contrastingly glabrous (Fig. 60).

Pronotum elongate, narrow, length/greatest width about 1.35; lateral margins nearly parallel, width at middle equal to that at base, apex only slightly narrowed; lateral margin not sinuate anterior to hind angle; outer carina narrowed and more or less bent outward at base; pronotum with about six marginal setae in most specimens (but only two in holotype); prosternum with well-developed precoxal carina extended at least halfway to anterior margin; carina bounded on either side by longitudinal impressions.

Elytral striae deep, coarsely punctate; intervals narrow, carinate; humerus prominent, quadrangular, with conspicuous patch of golden pilosity; Stria I with two setae near apex; Stria II with five setae; metasternum with many discal punctures coarser than marginal ones; margins of metasternum pilose.

Anterior femur with ventral tooth in both sexes; anterior tibia slender, with proximal tooth present in male, absent from female; cleaning organ with proximal spur small but distinct; as small triangular tooth on distal side of intermediate tooth; distal spur flattened; comb teeth short, slightly overlapping brushes. Male with hind calcar tapered, its tip truncate.

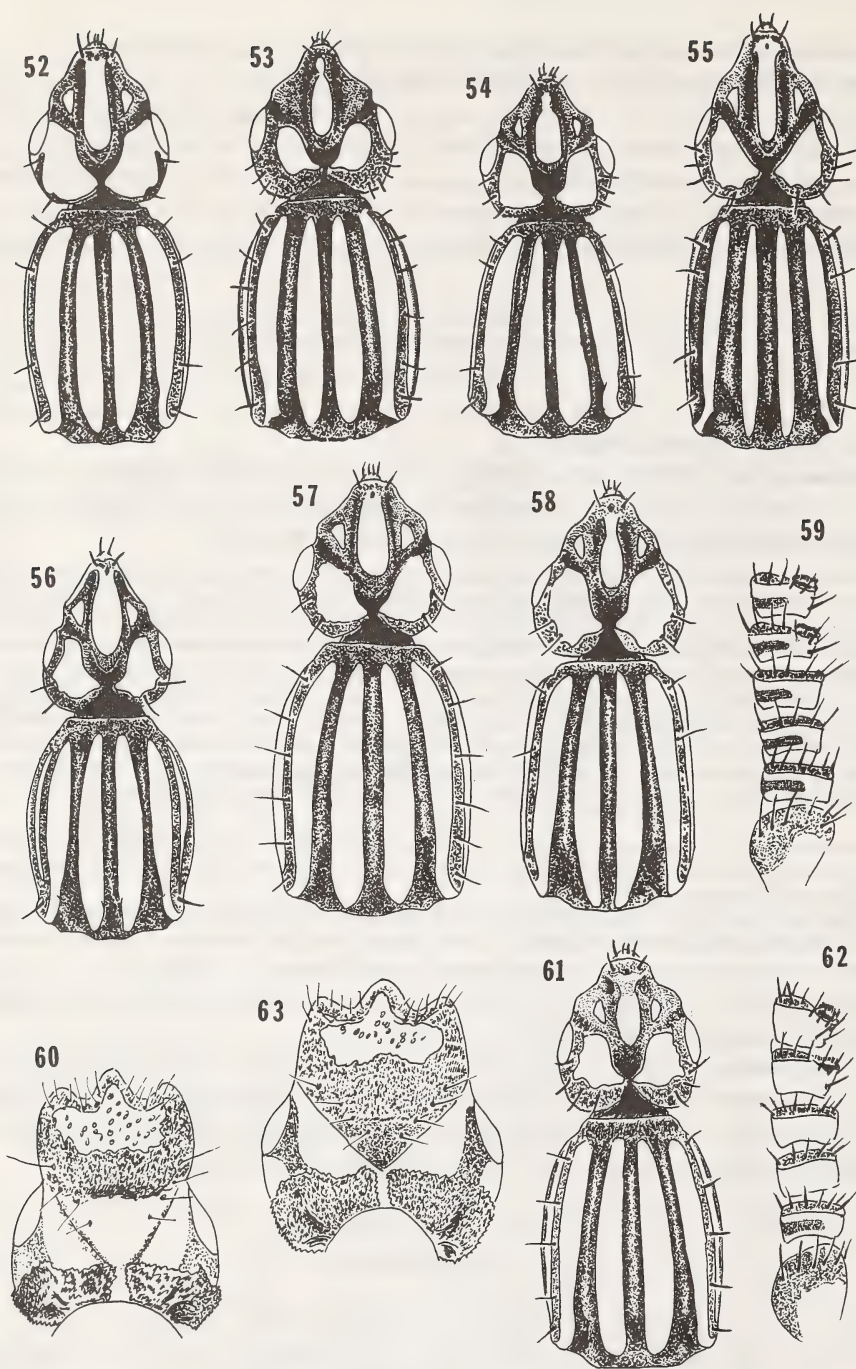
This species is similar to *G. gigas*, from which it differs in its smaller size, somewhat narrower body, and especially in having a well-developed precoxal carina.

Range. – The holotype, which is in poor condition, and without exact locality data, appears to us to be conspecific with a series of specimens from the northern tip of Madagascar, representing the following localities: Cap d’Ambre, coll. F. Schneider, one male (MNHN); Diego Suarez, collector not indicated, two females (MNHN); Mont Ambre, coll. Sicard, 1930, two males one female (MNHN).

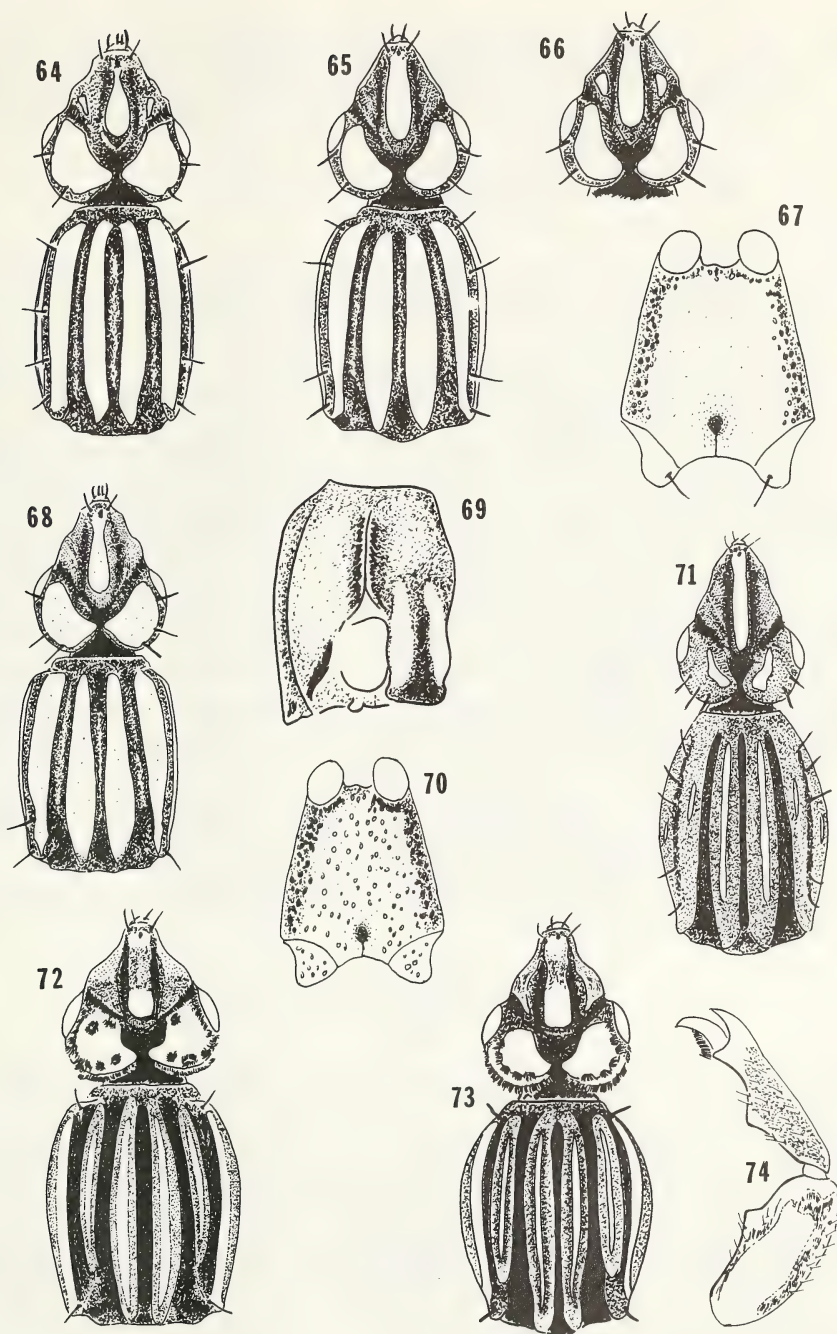
Grouvellina gigas new species
(Fig. 61-63)

Type material. – HOLOTYPE male, labelled: “MADAGASCAR, Chutes de la Mort, XI-10-1959, coll. E.S. Ross” (CAS). Thirteen PARATYPES (all from Madagascar) one female same data as type (CAS); one male, 1883, coll. Humblot, ex coll. Oberthur 1904-175 (BMNH); four males, six females, Ambodivoangy, 1959-1961, coll. J. Vadon (MRAC); one male, Madagascar Sud, 1901, coll. Alluaud (MNHN).

Description. – Length 8.0–10.5 mm, females averaging larger than males. Antennal Segment XI distinctly longer than wide; stylet prominent, conical, acute; tufts of minor hairs on Segments V–X; antennal Segment I with broad dorsal band of pollinosity; Segment II with two dorsal bands; Segments III–X with narrow apical pollinose bands, but without basal bands (Fig. 62).



Figures 52 – 63. Fig. 52-74, Genus *Grouvellina*; Fig. 52-58, Head and pronotum, dorsal aspect; Fig. 52, *G. montana* new species; Fig. 53, *G. hova* new species; Fig. 54, *G. cuneata* new species; Fig. 55, *G. radama* new species; Fig. 56, *G. divergens* new species; Fig. 57, *G. ranavalona* new species; Fig. 58-60, *G. tubericeps* (Fairmaire); Fig. 58, Head and pronotum, dorsal aspect; Fig. 59, Antennal Segments I-VI; Fig. 60, Head, ventral aspect; Fig. 61-63, *G. gigas*, new species; Fig. 61, Head and pronotum, dorsal aspect; Fig. 62, Antennal Segments I-VI; Fig. 63, Head, ventral aspect.



Figures 64 – 74. Fig. 64, Head and pronotum, dorsal aspect, *G. edentata*, new species; Fig. 65-67, *G. descarpentriesi*, new species; Fig. 65, Head and pronotum, dorsal aspect; Fig. 66, Head, dorsal aspect; Fig. 67, Metasternum, metacoxae; Fig. 68-70, *G. cooperi* new species; Fig. 68, Head and pronotum, dorsal aspect; Fig. 69, Prothorax, ventrolateral aspect; Fig. 70, Metasternum, metacoxae; Fig. 71-73, Head and pronotum, dorsal aspect; Fig. 71, *G. grouvellei* (Fairmaire); Fig. 72, *G. cinerea*, new species; Fig. 73, *G. dentipes*, new species; Fig. 74. Femur, tibia, male, *G. dentipes*, new species.

Head distinctly wider than long; labrum with four setae; frontal and postantennal grooves broad, pollinose; median lobe relatively short, broad, obtusely pointed posteriorly; frontal groove shallow, parafrontal bosses distinct; temporal lobes slightly wider than long, sinuate anterior to medial angles, latter apparently acute, because of pollinosity on the posterior surface; three to four temporal setae; orbital groove marked by broad, complete band of pollinosity; occiput and frontal pit with conspicuous reddish pilosity; three to four pairs of postlabial setae; postmentum pollinose, separating the glabrous shining genae (Fig. 63).

Pronotum elongate, length/greatest width 1.33; sides nearly parallel, widest point slightly posterior to middle; slightly narrowed at base, more distinctly at apex; lateral margin not at all sinuate anterior to hind angle; pronotal carinae convex, rather narrow; outer carina relatively broadly truncate at base, at most slightly bent outwards there; inner carina broadened or rounded at base; four to six marginal setae; precoxal carina absent.

Elytral striae deep, pollinose, coarsely punctured; intervals narrow, carinate; humerus prominent, quadrangular, with conspicuous patch of golden pilosity; base of second interval elevated; Stria I without setae; Stria II with five to seven setae; Stria IV with six to eight setae; Stria VII with four to five setae near apex; metasternum with many discal punctures, latter slightly coarser than marginals; metasternum with narrow lateral pilose strip.

Anterior femur with ventral tooth in both sexes; anterior tibia with proximal tooth in male, absent from female; cleaning organ with wide comb, strongly overlapped by brushes, comb teeth blunt; proximal spur stout, conical; distal spur small, hind calcar small, its tip blunt, spur clearly removed from calcar, small, acute.

Females of this species are among the largest of Rhysodini. *G. gigas* differs from *G. tubriceps* in its larger size and stouter form, in the absence of a precoxal carina, in the presence of the postmental pilosity and the absence of the dorsal basal pilose bands of antennal Segments III-X. It differs from *G. cuneata* in the shape of the pronotum and from *G. hova* in the presence of parafrontal bosses.

Variation. – Of the eighteen specimens we have studied, the following characters exhibit variation: shape of medial angle of temporal lobe, width of base of the inner carina, depth of the frontal grooves, extent of glabrous area of the parafrontal boss, elevation of bases of the third and fifth elytral intervals in addition to the second and degree of sinuation of the lateral margin of the humeral tubercle. However, there has been no consistent pattern of characters that would suggest another species in this group.

In addition, there is a male (MNHN) labelled: “Madagascar, Est, Presqu’île de Masoala, Hiaraka, XII-1968, coll. Vadon/Peyrieras” which resembles the type series except for reduction of orbital pilosity. The latter is very narrow, and is almost discontinuous anteriorly, leaving the bases of the temporal setae partly isolated in round clumps of pilosity. These, however, are in narrow contact with the pilosity of the orbital groove, and are not completely isolated as in *G. dentipes* and *G. cinerea*.

Final judgement of these aberrant forms will have to be held until there are more specimens available and better locality data recorded.

Grouvellina cuneata new species (Fig. 54)

Type material. – HOLOTYPE male, labelled: “MADAGASCAR: Tamatave et Forêt Alahakato, 1/VII, 1888, ex. coll. Breuning” (MRAC).

Description. – Length 7.2 mm. Antennal Segment XI distinctly longer than wide; stylet prominent, conical, 0.33 as long as segment; tufts of minor setae on Segments V-X; Segment I with broad dorsal band of pollinosity; Segment II with two transverse bands of pollinosity; Segments III-X each with apical pollinose band, but without basal one.

Head about as wide as long; labrum with four setae; frontal and postantennal grooves broad, pollinose; median lobe short, broad, obtusely rounded posteriorly; parafrontal bosses distinct; temporal lobes slightly longer than wide, sinuate anterior to medial angles, latter narrowly obtuse and narrowly separated; three to four temporal setae; orbital groove marked by broad, complete band of pollinosity; occiput and frontal pit with reddish pilosity; four pairs of postlabial setae; postmentum and most of mentum glabrous, shining, these areas separated by narrow transverse pollinose area.

Pronotum elongate, distinctly wedge-shaped; broadest just anterior to base, sides convergent anteriorly, apex narrow; length of pronotum/greatest width 1.33; pronotal carinae rather narrow; convex; inner carina broadest at base, pointed anteriorly; marginal carina narrower than in *G. tubriceps* and *G. gigas*; outer carina obliquely truncate at base; three marginal setae; precoxal carina absent.

Elytral striae conspicuously unequal; I-V impressed; I the narrowest, others successively wider to V, latter prominent and widely pilose; Stria VI reduced to row of isolated punctures anteriorly, punctures narrowly connected in posterior half; Stria VII irregularly curved, somewhat zigzag; intervals broader and less distinctly carinate than in *G. tubriceps* and *G. gigas*; humerus prominent, subrectangular, conspicuously pilose; Stria I with one seta in apical half; Striae II with three setae in apical half; Stria IV with six to eight setae; Stria VII with about five setae in apical fifth; metasternum with many coarse distal punctures, but without lateral pilosity.

Femur of anterior leg relatively slender, with ventral tooth; male with proximal tooth on anterior tibia; hind calcar very small, obtusely pointed, in rear view, doubly curved, so that its outline resembles the toe of a boot.

The most conspicuous marks of this species are the wedge-shaped pronotum, and the conspicuously unequal elytral striae and intervals.

Grouvellina hova new species

(Fig. 53)

Type material. – HOLOTYPE male, labelled: “MADAGASCAR: Tsaramainiandro, X-1950, coll. J. Vadon” (MNHN). Three PARATYPES two males, same data as type (MNHN); one male labelled: “Madagascar” coll. Humblot 1885 (MNHN).

Description. – Length 8.7–9.0 mm (only males are known; if the females are conspicuously larger than males, as in *G. gigas*, they may be the largest member of the genus). Antennal Segment XI distinctly longer than wide, stylet conical, acute; tufts of minor setae on Segments V–X; antennal Segment I with broad dorsal band of pollinosity; Segment II with two transverse pollinose bands; Segments III–X with apical but not basal bands.

Head short, clearly wider than long; labrum with four setae; frontal, postantennal grooves broad, pollinose; median lobe short, broadly rounded posteriorly; parafrontal bosses absent, superantennal area entirely pollinose; temporal lobes transverse, wider than long, markedly sinuate anterior to medial angle, latter apparently acute, because of pollinosity on posterior surface; five to six temporal setae; orbital groove marked by very broad band of pollinosity; occiput and frontal groove with conspicuous pilosity; three pairs of postlabial setae; postmentum pollinose.

Pronotum shorter than in *G. gigas*, length/greatest width 1.25; greatest width near middle, sides curved; apex strongly narrowed, base slightly narrowed; lateral margin slightly sinuate anterior to hind angles; pronotal carinae convex, rather narrow; outer carina rather broadly, obliquely truncate at base; marginal carina narrow, nearly vertical; five to six marginal setae; precoxal carinae absent.

Elytral striae deep, coarsely punctate; intervals narrow, carinate; humerus prominent, subrectangular, conspicuously pollinose; Stria I without setae; Stria II with about ten setae; Stria IV with about nine setae; Stria VII with about five in its apical fifth; metasternum with many discal punctures which are as coarse as lateral punctures; metasternum without lateral pollinosity.

Anterior femur with ventral tooth; male with proximal tooth on anterior tibia (female unknown); cleaning organ with comb hairs in line with brush hairs, indistinctly differentiated from them and not overlapping them; both spurs of anterior tibia present, small, acute; calcar of hind leg truncate, flattened.

This very large species resembles *G. gigas*, but is more stoutly built, and is easily distinguished by complete absence of the parafrontal bosses. *G. cooperi* and most specimens of *G. descarpentriesi* also lack the bosses, but differ from *G. hova* in being much smaller, in lacking the femoral tooth, and in having the head elongate.

Grouvellina ranavalona new species

(Fig. 57)

Type material. – HOLOTYPE female, labelled: “MADAGASCAR, cn. Fairmaire” (MNHN). PARATYPE female, labelled: “MADAGASCAR 1901-267” (BMNH).

Description. – Length 9.7–10.0 mm. Antennal Segment XI longer than wide; stylet large, conical, acute; tufts of minor setae present on Segments V–X; antennal Segment I with broad dorsal band of pollinosity; Segment II with two transverse pollinose bands; Segments III–X with apical pollinose bands but without basal ones.

Head slightly wider than long; labrum with four setae; frontal and postantennal grooves broadly pollinose; median lobe short, broadly rounded posteriorly; parafrontal bosses distinct; temporal lobes slightly longer than wide; medial angles obtuse, narrow; two to three temporal setae; orbital groove marked by broad, complete band of pollinosity; occiput and frontal pit with conspicuous pollinosity; three to four pairs of postlabial setae; mentum nearly impunctate, glabrous except for narrow posterior transverse strip of pollinosity; postmentum also glabrous.

Pronotum relatively shorter than in *G. gigas*, length/greatest width 1.26; pronotum widest near middle, sides curved; apex strongly narrowed, base slightly so; margin not sinuate anterior to hind angles; pronotal carinae convex, rather narrow; outer carinae narrowed and abruptly divergent at base; five to six marginal setae; precoxal carina absent.

Elytral striae deep, coarsely punctured; intervals narrow, carinate, humeral tubercle prominent, conspicuously pilose; Stria I with one seta near apex; Stria II with four setae in apical half; Stria IV with seven to eight setae; Stria VII with about nine setae in apical fourth; metasternum with many discal punctures, latter finer than marginal ones; metasternum with some lateral pollinosity.

Anterior femur of female without ventral tooth, but with rounded swelling; male unknown.

This is a very large, broad-headed species similar to *G. gigas* and *G. hova*, but differing from both in the absence of a ventral tooth on the anterior femur.

Grouvellina edentata new species

(Fig. 64)

Type material. — HOLOTYPE male, labelled: "MADAGASCAR, 1885, coll. Humblot no. 85/6044" (MNHN). PARATYPES three males, same data (MNHN).

Description. — Length 5.0–6.0 mm. Antennal Segment XI slightly longer than wide; stylet short, conical; tufts of minor setae on Segments V–X; Segment I with broad dorsal pollinose band; Segments II–X with narrow apical bands but no basal ones.

Head slightly longer than wide; four labral setae; frontal and postantennal grooves deep; median lobe broadly rounded at apex; parafrontal bosses distinct, narrow, elongate; temporal lobes slightly longer than wide, rather shallowly sinuate anterior to medial angles; latter obtuse; two temporal setae; orbital groove marked by narrow but complete band of pollinosity; two to three pairs of postlabial setae.

Pronotum elongate, length/greatest width 1.40; widest near middle, sides slightly curved; base and apex only moderately narrowed; lateral margin not sinuate anterior to hind angle; pronotal carinae rather broad, convex; inner carina widest near middle, base and apex nearly equally tapered; outer carina obliquely truncate at base, but not divergent; three marginal setae; precoxal carina present.

Elytral striae fine, shallow, very coarsely punctured; intervals convex but not carinate; base of Interval II elevated in form of small, indistinct tooth; humeral tubercle rather small; Stria I with two to four setae in apical fifth; Stria II with two to three setae in apical fourth; Stria IV with four to six setae; Stria VII with about five setae near apex; metasternum with scattered discal punctures, latter finer than lateral ones; metasternum not pilose laterally.

Anterior femur without ventral tooth; anterior tibia without proximal tooth (male); cleaning organ with comb teeth not flattened; distal spur of front tibia large; proximal one absent; male with calcar of hind leg acuminate, with narrow base, very close to spur, latter large. Female unknown.

This is the smallest species in the genus. It has a complete, though narrow, orbital groove. It is most similar to *G. cooperi*, from which it differs in having a distinct parafrontal boss, and in having the inner pronotal carinae less narrowed anteriorly.

Grouvellina cooperi new species

(Fig. 68–70)

Type material. — HOLOTYPE female, labelled: "MADAGASCAR, coll. Rogez" (MCZ).

Description. — Length 6.9 mm. Antennal Segment XI slightly longer than wide; stylet conical, acuminate; tufts of minor setae on Segments V–X; Segments I, II broadly pollinose dorsally; Segments III–X with apical pollinose bands but no basal ones.

Head longer than wide; labrum with four setae; frontal and postantennal grooves deep; median lobe tapered anteriorly, widest near broadly rounded apex, parafrontal bosses absent, superantennal area entirely pollinose; temporal lobes distinctly longer than wide, rather shallowly sinuate anterior to medial angles; latter obtuse; three temporal setae; orbital groove marked by narrow but complete band of pollinosity; three to four pairs of postlabial setae.

Pronotum narrow, elongate, length/greatest width about 1.33; pronotum widest distinctly anterior to middle; sides curved, moderately narrowed at apex, slightly less so at base; lateral margin slightly sinuate anterior to hind angle; pronotal carinae broad, rather convex; inner carina widest in basal fourth, apex strongly tapered; outer carina with extreme base markedly narrowed, but not divergent; marginal setae 0, or one, located near angular seta; precoxal carina well developed, nearly extended to anterior margin (Fig. 69); postcoxal tooth large, blunt.

Elytral striae deep, narrow, coarsely punctate, punctures wider than striae; inner intervals nearly flat; outer ones more convex; base of Interval II in form of distinct tooth; humeral tubercle slightly prominent, pollinose; Stria I without setae; Stria II with one seta near base and another near apex; Striae IV and VII without setae; metasternum coarsely punctate, discal punctures equal in size to marginal ones; metasternum with lateral pilose strips (Fig. 70).

Anterior femur without ventral tooth; both spurs distinct on anterior tibia; anterior and middle femora and all tibiae with many more setae than in other members of genus. Male unknown.

This species is a small one with a complete, though narrow orbital groove. It differs from *G. edentata* in lacking the parafrontal boss. In the latter feature, it resembles *G. hova*, but the latter species is much larger, has carinate elytral intervals, and a ventral tooth on the anterior femur, and lacks a precoxal carina. Most specimens of *G. descarpentriesi* also lack a parafrontal boss. These can be distinguished

from *G. cooperi* by the absence of the outer labral setae and the precoxal carina.

It is a pleasure to dedicate this species to Dr. Kenneth Cooper, whose contributions to entomology have been multiple in both place and time.

Grouvellina montana new species

(Fig. 52)

Type material. – HOLOTYPE male, labelled: “MADAGASCAR; coll. C. Schauf” (MNHN), written in Grouvelle’s hand “*R. montanus*, type”. This name was not published. PARATYPES three females, labelled: “MADAG.” (MNHN).

Description. – Length 6.2–7.0 mm. Antennal Segment XI twice as long as wide; stylet acute; tufts of minor setae on Segments V–X; Segment I with broad dorsal pollinose band; Segment II with basal and apical band, separated by narrow glabrous band; Segments III–X with apical bands but without basal ones.

Head slightly longer than wide; labrum with four setae; frontal and postantennal grooves deep; median lobe nearly parallel-sided, its apex slightly broadened and rounded; parafrontal bosses distinct, triangular; temporal lobe slightly longer than wide, medial margin shallowly sinuate anterior to obtuse medial angle; two temporal setae; orbital groove incomplete; pollinosity absent anterior to anterior temporal seta, with glabrous area of temporal lobe extended to eye; five pairs of postlabial setae in pilose transverse band which separates glabrous submentum from mentum.

Pronotum elongate, length/greatest width 1.35, widest anterior to middle, moderately narrowed both to base and apex; side not sinuate anterior to hind angle; pronotal carinae broad, flat; extreme base of outer carina narrowed and divergent at hind angle; two to three marginal setae, most anterior one near anterior angle; precoxal carina absent.

Elytral striae shallow, narrower than intervals, rather finely punctate; intervals slightly convex near base, otherwise nearly flat; Stria VI not impressed, marked only by a row of punctures; humeral tubercle narrow but prominent; Stria I with one seta near apex; Stria II with four in apical fifth; Stria IV with four to five setae; Stria VII with about six setae in apex; metasternum without discal punctures, without pollinosity except in each marginal puncture.

Anterior femur with ventral tooth; that of male large, that of female small and partly concealed by pollinosity; male with large proximal tooth on anterior tibia; female without such tooth; cleaning organ with comb comprised of short distinctly flattened teeth; proximal and distal spurs both rather large; male with acutely pointed hind calcar; female with spurs of middle and hind tibiae very unequal, anterior ones much reduced.

This is a distinctive small species with an incomplete orbital groove, a feature distinguishing it from all other species of *Grouvellina*. Absence of a precoxal carina and presence of a femoral tooth distinguish it from *G. edentata* and *G. cooperi*.

Grouvellina radama new species

(Fig. 55)

Type material. – HOLOTYPE male, labelled: “MADAGASCAR: Mahatsinjo près Tananarive” (MNHN). Six PARATYPES one male, same data as type (MNHN); one male, labelled: “MADAGASCAR: Antsianaka, 1923, acq. Le Moul’t” (AMS); one female, labelled: “MADAGASCAR, forêt de Fito, ex. coll. Dr. Breuning” (MRAC); one male, two females, labelled: “MADAGASCAR, ex. col. Le Moul’t” (MRAC).

Description. – Length 7.5–8.9 mm. Antennal Segment XI slightly longer than wide; stylet short, conical; tufts of minor setae on Segments V–X; Segments I, II broadly pilose dorsally; Segments III, IV with broad apical pollinose bands; Segments V, VI with narrow ones; Segments VII–X each with two transverse rows of pollinose spots.

Head distinctly longer than wide, preocular portion elongate; labrum with two setae; frontal and postantennal grooves deep; median lobe very narrow, its sides parallel, its tip rounded; parafrontal bosses distinct; temporal lobe longer than wide; margin scarcely sinuate anterior to obtuse medial angle; five temporal setae; orbital groove represented by complete pollinose band; many pairs of postlabial setae, of two distinct sizes; postmental area pollinose; mentum glabrous with scattered punctures.

Pronotum elongate, length/greatest width 1.35; widest near middle, sides almost parallel, base and apex only slightly narrowed; lateral margin slightly sinuate anterior to hind angles; parafrontal carinae very narrow, scarcely wider than the grooves, convex; inner carinae straight, pointed at both ends; outer carina obtuse at apex, its base narrow, and divergent; two to three marginal setae; precoxal carina fine, extended about halfway to anterior margin; prosternum with very deep medial pit; one specimen with pair of prosternal setae near anterior ends of carinae.

Elytral striae very broad, very coarsely punctured, expanded opposite base of each puncture; intervals narrow, less than half as wide as striae, scarcely carinate, expanded punctures making the intervals appear segmented, slightly zigzag; humeral tubercle small; Stria I with one seta at apex; Stria II with five to six apical setae; Stria IV with eight setae; apical tubercle with two setae; Stria VII with about six setae in apical fifth; metasternum with lateral pollinose strips and with coarse discal punctures.

Anterior femur without ventral tooth; male without proximal tooth on anterior tibia; cleaning organ with stiff comb teeth near middle gradually graded to long brush hairs on either side (not graded abruptly as in other species); distal spur well developed; proximal spur vestige at base of intermediate tooth; hind calcar rather long, its dorsal and ventral margins nearly parallel, its tip truncate.

This large species has a distinctive long, narrow, parallel-sided median lobe, duplicated only in the otherwise very different *G. grouvellei*. The pronotal carinae are narrower than in other species. The most similar species is *G. divergens*, which has a similarly elongated head, but which has a wide median lobe, and lacks the precoxal carinae.

Grouvellina descarpentriesi new species
(Fig. 65-67)

Rhysodes tubriceps auct. nec. Fairmaire. Both Grouvelle (1903) and Arrow (1942) interpreted this species as *R. tubriceps*.

Type material. – HOLOTYPE male, labelled: "MADAGASCAR, Annanarivo (Sikora)" (MNHN). 18 PARATYPES (all from Madagascar) as follows; one female, same data as type; one male, two females, Antananal; one female, Antananarivo; one male, three females (on same pin), Madagascar, Sikora; four males, one female, "Madagas" (all MNHN); one female, "Madagas". Fry Colln. 1905-100 (BMNH); one female, "Madagas". 79.18 (BMNH); one female, forêt de Fito, ex. coll. Dr. Breuning (MRAC); one female, "Madagas., ontv. 6 April 08, Ant. Grouvelle" (LEI).

Description. – Length 6.1–8.0 mm. Antennal Segment XI almost twice as long as wide; stylet long, acute, about 0.33 total length of segment; tufts of minor setae on Segments V–X; Segment I and II with broad dorsal pollinose band; Segments III–V with narrow apical pollinose bands; Segments VI–X with apical pollinose bands and basal transverse rows of pollinose spots.

Head longer than wide; preocular portion elongate; labrum with two setae; frontal grooves deep, rather broad, postantennal grooves deep; median lobe moderately broad, slightly broadened posteriorly, tip broadly rounded; parafrontal boss variable, in most specimens absent, in few specimens suggested by small, irregular glabrous areas; temporal lobe longer than broad; margin shallowly sinuate anterior to medial angles, latter obtusely rounded, margin not emarginate posterior to medial angle; two temporal setae; orbital groove marked by rather narrow band of pilosity; two pairs of postlabial setae; mentum with lateral margins pilose, remainder glabrous; postmentum glabrous, separated from genae and mentum by narrow pollinose band.

Pronotum elongate, narrow, length/greatest width 1.35; widest point anterior to middle, apex scarcely narrower than base; margin shallowly sinuate anterior to hind angles; pronotal carinae rather narrow, convex, only slightly broader than paramedian grooves; outer carina narrowed and abruptly divergent at base; three marginal setae, most anterior one near anterior angle; precoxal carina represented by small rudiment between two precoxal pits.

Elytral striae moderately broad, slightly wider than intervals, coarsely, closely punctate; striae dilated around each puncture, intervals of irregular width; intervals convex but not carinate; base of Interval II raised in form of small "tooth"; humeral tubercle moderately prominent; Stria I without setae; Stria II with two near apex; Stria IV with five setae; Stria VII with five setae in apical fifth; metasternum with lateral punctures but without discal ones or lateral pilosity (Fig. 67).

Anterior femur without ventral tooth; male without proximal tooth on anterior tibia; cleaning organ with central comb sharply distinct from overlapping brushes on hairs at either end; distal spur well developed; proximal spur absent; hind calcar of male very small, blunt; hind femur of male sinuate ventrally.

This is a moderate-sized species with an elongate head. It is most similar to *G. radama*, but the latter is larger, has a narrower, more elongate median lobe and much narrower pronotal carina, as well as having a well-developed precoxal carina. *G. divergens* is also similar to *G. descarpentriesi*, but differs in the shape of the medial angle of the temporal lobe, in lacking a tuft of minor setae on antennal Segment V, and in having the marginal carina of the pronotum abbreviated posteriorly.

Of the 20 specimens studied, two have a distinct parafrontal boss. They are labelled as follows; one male, "Madagascar, Centre, Pays Betsileo, Route du Sud, km. 292, 1700m., 14/15-II-1974, P. Viette et A. Peyrieras" (MNHN) (Fig. 66); one female, "Madagascar, int. austr. Hildebrandt S." (MNH). We

have tentatively identified these as *G. descarpentriesi* based on the other species characters, but have not made them paratypes. More specimens are needed to determine whether or not this is a distinct species.

It is a pleasure to dedicate this species to Dr. A. Descarpentries of the Museum National d'Histoire Naturelle, Paris, whose generous aid during our study of the Grouvelle Collection was vital to the completion of this work.

Grouvellina divergens new species

(Fig. 56)

Type material. – HOLOTYPE male, labelled; “MADAGASCAR, Mt. d'Ambre, 1930, coll. Sicard” (MNHN). Nine PARATYPES one female, same data as type (MNHN); one female, same locality as type, Dec. 1900 (MNHN); four females, Mt. d'Ambre, no date (MNHN); one male, two females labelled: “MADAGASCAR, Diego-Suarez, 1893, coll. C. Alluaud” (MNHN).

Description. – Length 6.0–8.4 mm. Antennal Segment XI slightly longer than wide; stylet short, conical; tufts of minor setae present on Segments VI–X (absent from Segment V); basal setae absent from Segments V and VI; Segments I–II broadly pilose dorsally; Segments III–V with broad apical pollinose band; Segments VII–X each with two transverse rows of pollinose spots.

Head slightly longer than wide; preocular part narrow; slightly elongate; labrum with two setae; frontal and postantennal grooves deep; median lobe broad, dilated, its tip very broadly rounded; parafrontal bosses distinct; temporal lobe slightly longer than wide, its margin rather deeply sinuate anterior to medial angles, latter apparently acute, partly because of occipital pilosity; margin posterior to medial angles distinctly emarginate; two to three temporal setae; orbital groove represented by rather narrow band of pollinosity, its medial margin irregular; two pairs of postlabial setae; sides of mentum pilose; submentum pilose in most specimens, small glabrous median area present in others.

Pronotum moderately elongate; length/greatest width 1.31; widest anterior to middle, base moderately narrowed, apex rather markedly so; lateral margin sinuate anterior to hind angle; pronotal carinae moderately narrow, convex; outer carina narrowed and abruptly divergent at base; marginal carina abbreviated posteriorly; marginal setae absent, angular seta present; precoxal carina absent.

Elytral striae broad, slightly wider than intervals; latter convex, subcarinate; borders of intervals slightly irregular; humeral tubercle rather small, Stria I with three setae in apex; Stria II with six setae in apical half; Stria IV with six setae; Stria VII with about six in apical fifth; metasternum with discal punctures much finer than marginal ones; metasternum without lateral pollinose strips.

Anterior femur without ventral tooth; male without proximal tooth on anterior tibia; cleaning organ with comb teeth conical, not flattened, graded gradually to brush hairs on either side, rows not overlapping; both spurs of anterior tibia well developed; hind calcar small, more or less pointed, only slightly larger than spur.

This is a moderate-sized species, superficially like *G. radama* and *G. descarpentriesi*, but differing from them in the absence of minor setae from antennal Segment V. In the latter feature it resembles only *G. grouvellei*.

Grouvellina grouvellei (Fairmaire)

(Fig. 71)

Rhysodes grouvellei Fairmaire, p. 10

Type material. – LECTOTYPE (here designated) male, labelled: “MADAGASCAR” (MNHN). PARALECTOTYPE one female, labelled: “MADAGASCAR, Fry Coll. 1905-100”, labelled as “cotype” (BMNH).

Description. – Length 7.0–8.8 mm. Antennal Segment XI longer than wide; stylet conical, short; tufts of minor setae on Segments VI–X (absent from Segment V); basal setae absent from Segment V; Segment I with most of dorsal surface pilose; Segment II with pollinose band; Segments III–V with narrow apical pollinose band; Segment VI with apical band and basal row of pilose spots; Segments VII–X with two rows of pilose spots.

Head distinctly longer than wide, preocular portion narrow, elongate; labrum with two setae; frontal and postantennal grooves deep; median lobe very long, narrow, its sides parallel, its tip obtusely rounded; parafrontal boss absent from lectotype but well developed in paralectotype; temporal lobe longer than broad, its medial angles obtuse; glabrous area of temporal lobe very small, less than 0.33 of total width of temporal lobe; three to four temporal setae; two to three pairs of postlabial setae; sides of mentum and entire postmentum pollinose; mentum with scattered pilose punctures.

Pronotum rather narrow, elongate, length/greatest width 1.36; widest anterior to middle; base moderately narrow, apex more strongly so; margin with long shallow sinuation anterior to hind angle; median and paramedian grooves deep, wide; marginal groove incomplete, closed both anteriorly and posteriorly, confined to middle third of pronotum; pronotal carinae extensively pollinose, inner carina with narrow glabrous space extended most of length; outer carina with traces of interrupted linear glabrous area; marginal carina with small glabrous area near middle of length; four to five marginal setae; rudimentary precoxal carina present; postcoxal tooth small.

Elytral striae shallow, with very coarse deep punctures; intervals nearly flat, almost entirely pollinose, except for narrow strip along suture and narrow, irregular discontinuous strips on Intervals II and III and on apical tubercle and traces in some of the outer intervals; some of the striae punctures also glabrous; humeral tubercle small; Stria I with two setae near apex; Striae II with about twelve setae (some displaced laterad to stria); Stria IV with about ten setae (some displaced laterad to stria); Stria VI with about twelve setae; about six setae on apical tubercle; about seven in apical fifth of Stria VII; metasternum with discal punctures finer than marginal ones; metasternum with lateral pollinose strip.

Anterior femur without ventral tooth; proximal tooth absent from anterior tibia of male; all femora unusually long and slender for genus; cleaning organ with central row of comb teeth overlapped at either end by row of slender brush hairs; distal spur well developed; proximal one absent; hind calcar slender, tapered, its tip blunt.

This species is easily recognized by the abbreviation of the marginal groove and by the extensive development of the pollinosity, which covers almost the entire dorsal surface.

Variation. – As aforementioned, the parafrontal boss is absent from the lectotype, but well developed in the paralectotype. As for *G. descarpentriesi*, two species may be represented, but more specimens will be needed to make certain. In addition to the type series, we have seen two other specimens, a male labelled: “MADAG.” (MNHN), and another male, labelled: “MADACASCAR: Annanarivo (Sikora)” (MNHN). Both of these specimens lack the parafrontal boss.

Grouvellina dentipes new species

(Fig. 73, 74)

Type material. – HOLOTYPE male, labelled: “MADAGASCAR: Fizonzo; IX, 1959, coll. J. Vadon” (MRAC).

Description. – Length 7.8 mm. Antennal Segment XI slightly longer than wide; stylet conical, large, rather blunt; tufts of minor setae present on Segments V-X; Segment I with broad dorsal pollinose band; Segment II with partly confluent basal and apical pollinose bands; Segments III-V with both basal and apical bands; Segment VI with basal band and apical row of pilose spots; Segments VII-VIII similar, but with apical spots much reduced; Segments IX, X with basal band but no apical spots or bands.

Head wider than long; labrum with two setae; postantennal and frontal grooves deep; median lobe short, broad, parallel-sided, abruptly truncate posteriorly; anterior third of median lobe finely pollinose; parafrontal boss absent, superantennal area entirely pollinose; temporal lobe broader than long; margin deeply sinuate anterior to narrow, distinct medial angle; orbital groove represented by narrow but complete strip of pilosity; row of five prominent round tufts medial to it, each more or less concealing a temporal seta; two pairs of postlabial setae.

Pronotum very short for genus, length/widest width 1.20; pronotum widest anterior to middle, moderately narrowed to base, markedly narrowed to apex; margin distinctly sinuate anterior to hind angle; pronotal carinae convex, narrow, their margins pollinose, centers glabrous; inner carina entire; outer carina abbreviated at basal fifth of pronotum; marginal groove narrow, confluent with paramedian groove at base of outer carina; marginal carina entire, broader than outer carina; pronotum with angular seta, and one marginal on each side, near anterior angle; precoxal carina represented by small rudiment, between two precoxal pits.

Elytral striae broad, deep, coarsely punctate; intervals narrow, convex, subcarinate less than half width of striae; humeral tubercle small; Stria I with four setae in apical fifth; Stria II with two near apex; Stria IV with five; Stria VII with four in apical fifth; metasternum with discal punctures coarser than marginal ones; metasternum with lateral pilose strip; Sternite V with deep large lateral pits.

Anterior femur with large ventral tooth; male with large proximal tooth on anterior tibia (Fig. 74) (female unknown); hind calcar of male tapered, prominent, its tip truncate.

The abbreviated outer pronotal carina and the conspicuous tufts on the temporal lobe separate this species from all others excepting *G. cinerea*. From the latter it is easily distinguished by the large ventral tooth on the anterior femur.

Grouvellina cinerea new species

(Fig. 72)

Type material. – HOLOTYPE male, labelled: “MADAGASCAR: Perinet, sur Tavolo, 16-1-64, Rec. Brunck, coll. CTFT No. 111” (BMNH).

Description. – Length 9.2 mm. Antennal Segments X-XI missing from holotype; tufts of minor setae begin on Segment V; Segment I with broad band of pollinosity; Segment II with broad basal band; Segments III-V each with broad basal and apical bands, separated by narrow glabrous bands; Segment VI with basal band and trace of apical band; Segments VII-IX with basal band but without apical band or spots.

Head wider than long; labrum with two setae; postantennal and frontal grooves deep; median lobe short, broad, parallel-sided, its middle third pollinose, its tip truncate; parafrontal boss absent; superantennal area pollinose anteriorly, more pilose posteriorly; temporal lobe broader than long; margin deeply sinuate anterior to medial angle; latter blunt, broader than in *G. dentipes*; orbital groove represented by narrow strip of pollinosity, isolated tufts medial to it, one or two anterior tufts, and three to four tufts in form of transverse row posteriorly, each tuft more or less concealing a temporal seta; four pairs of postlabial setae.

Pronotum rather short, length/greatest width is 1.27; widest anterior to middle, moderately narrowed to apex and to base; margin slightly sinuate anterior to hind angle; pronotal carinae convex, narrow, glabrous at center, both inner and outer margins pollinose; inner carinae entire; outer carina abbreviated at basal fifth of pronotum; marginal groove narrow, confluent with paramedian groove at base of outer carina; marginal carina entire, broader than outer carina; pronotum with angular seta and one marginal located near anterior angle; precoxal carina represented by rudiment between two precoxal pits.

Elytral striae broad, deep, coarsely punctate; intervals narrow, convex, subcarinate, less than half width of striae; intervals distinctly unequal II, IV, V, and especially III, dilated at base; II very narrow posteriorly, its glabrous area more or less interrupted; Interval IV abbreviated posteriorly, distinctly shorter than III; humeral tubercle small; Stria I with two setae near apex; Stria II with one near apex; Stria IV with five setae; Stria VII with about five in apical fifth; metasternum with coarse discal punctures; metasternum with lateral pilose strip; Sternite V with large deep lateral pits.

Anterior femur without ventral tooth; male without proximal tooth on anterior tibia (female unknown); hind calcar of male very small, acutely pointed.

This species is similar in most respects to *G. dentipes*, but differs in the absence of the anterior femoral and proximal tibial teeth.

SUBTRIBE OMOGLYMMIINA

Description. – Part I, 66.

Key to Genera. – Part I, 66–67.

Genus *Xhosores* Bell and Bell 1978

Type species. – *Rhysodes figuratus* Germar 1840

Description. – Part I, 67. Only one species is known.

Xhosores figuratus (Germar 1840)

Rhysodes figuratus Germar 1840: 352.

Type material. – We have studied a male specimen from MNHB believed to be the type. It is labelled “CAP,43699”.

Genus *Yamatosa* NEW NAME

(Fig. 75-85)

Yamatoa Bell 1977, nec Kiriakoff 1967. We are grateful to Dr. Takehiko Nakane for pointing out this synonym.

Type species. – *Rhysodes niponensis* Lewis 1888.

Description. – Antennal Segment XI with stylet minute or absent; base of antennal Segment III more or less elongate; Segments V-X wider than Segments II-IV; minor setae in form of subapical rings on Segments V-X; basal setae absent; labrum with two setae; frontal, antennal grooves narrow; orbital grooves absent; clypeal setae one pair; temporal setae absent; postlabial setae one or two pairs.

Pronotum with basal impression on each side, preceded by discal striole; basal impression with tubercle; disc of pronotum continued laterad to basal impression, in form of basilateral lobe; basal impression partly closed posteriorly by "brace" laterad to inner lobe of base; marginal groove of pronotum single, fine, in most species ended anteriorly near anterior margin of pronotum (but reduced in *Y. reitteri*); pronotal setae absent.

Elytral striae coarsely punctured; basal scarp of elytron transverse medially; humeral tubercle present; elytral setae absent from Stria II, confined to apex of Stria IV or else absent; metasternum with marginal punctures; abdominal sterna with transverse bands of punctures; lateral pits present in both sexes, in most species confined to Sternum IV, in a few species also present on Sternum V; Sternum VI without setae.

Middle and hind tibiae each with two spurs; calcar of middle leg of male acute, directed distomedially; hind calcar blunt.

The genitalia of *Y. reitteri* have been described and figured (Part I, 68-69).

Lack of paramedian grooves separates this genus from most others in Subtribe Omoglymmiina. *Shyrodes* and *Srimara* appear to be related to *Yamatosa*, or perhaps represent highly specialized offshoots of it. Both *Shyrodes* and *Srimara* have ocelliform compound eyes, and have the basal scarp of the elytron modified. In *Yamatosa* the eyes may be fully developed or reduced, but are not ocelliform, and the basal scarp is transverse. *Plesioglymmius* is another genus which does not have complete paramedian grooves, but differs from *Yamatosa* in having only one spur on each middle and hind tibia. In *Plesioglymmius*, all species except *P. jugatus* have the discal striae dilated, and not linear.

This genus is confined to the Oriental Region, from the Himalaya to Japan, Taiwan, and Java.

Phylogeny. – With the exception of *Y. arrowi*, the species of *Yamatosa* are grouped clearly into an "Eastern Line" and a "Western Line". In the Eastern Line (*Y. niponensis*, *Y. longior*, and *Y. peninsularis*), the antenna has a distinct apical stylet, there is a beard of setae on the mentum of the male, and there are distinct lateral pits on abdominal Sternum IV, but not on Sternum V. In the Western Line, the antennal stylet is absent, the beard is absent, and there are lateral pits on both abdominal Sternum IV and V. *Y. boysi*, *Y. draco* and *Y. reitteri* belong to the Western Line, known only from the Himalaya. *Y. arrowi*, despite its being a Himalayan species, clearly belongs to the Eastern Line.

Among the species of the Eastern Line, *Y. longior* and *Y. peninsularis* are clearly closely related, both having a precoxal carina, short discal striae, and, in the male, the anterior tibia grooved medially. In *Y. longior*, both sexes have a bearded mentum, while the female of *Y. peninsularis* is unknown. In *Y. niponensis*, the precoxal carina is absent, the discal striole is long, the beard is present in the male but absent from the female, and the anterior tibia of the male is not grooved. The relationships of *Y. arrowi* are somewhat problematical, partly because the male is unknown. The absence of a precoxal carina and the long discal striole seem to link it to *Y. niponensis*, while the presence of a beard in the female is a character shared with the two preceding species. It also differs from all other members of the genus in several characters, including large size, broad-based pronotum, dilated frontal grooves, and enlarged anterior tentorial pits.

Among the species of the Western Line, *Y. boysi* and *Y. draco* are clearly closely related to one another. Both species have reduced eyes, and probably both are flightless (*Y. boysi* has vestigial hind wings, while *Y. draco* has not yet been checked for this character). Both species have one seta each in the apex of Striae II and IV of most specimens, while such setae are not found in other species of *Yamatosa*.

Y. reitteri is a more isolated species. Unlike the two preceding species, it has full-sized eyes and hind wings. It has two specializations not seen in any other member of the genus: the marginal groove of the pronotum has been reduced to a basal remnant, while the male has lost the ventral tooth of the anterior femur.

KEY TO SPECIES

- | | | |
|--------|--|--|
| 1 | Segment XI of antenna with distinct apical stylet; both eye and marginal groove of pronotum fully developed..... | 2 |
| 1' | Segment XI of antenna obtuse, without apical stylet; either eye reduced or else marginal groove of pronotum reduced..... | 5 |
| 2 (1) | Prosternum with distinct precoxal carinae; discal striole ended at or posterior to middle of pronotum | 3 |
| 2' | Prosternum without precoxal carinae; discal striole ended at or anterior to apical third of pronotum | 4 |
| 3 (2) | Precoxal carina extended more than 75% of distance from coxa to anterior margin of prosternum; discal striole 50% pronotal length..... | <i>Yamatosa longior</i> (Grouvelle), p. 425 |
| 3' | Precoxal carina, extended about 33% of distance from coxa to anterior margin of prosternum; discal striole 33% pronotal length..... | <i>Yamatosa peninsularis</i> (Arrow), p. 427 |
| 4 (2') | Frontal and antennal grooves narrow, equal in width to posterior part of clypeal grooves; posterior margins of frontal and antennal grooves sharply defined; discal striole ended at anterior third of pronotum | <i>Yamatosa niponensis</i> (Lewis), p. 427 |
| 4' | Frontal and antennal grooves dilated, much wider than posterior part of clypeal grooves; posterior margins of frontal and antennal grooves not sharply defined; discal striole extended nearly to anterior margin of pronotum..... | <i>Yamatosa arrowi</i> (Grouvelle), p. 428 |
| 5 (1') | Marginal groove of pronotum absent except in basal fourth of pronotum; eyes large, much deeper than long | <i>Yamatosa reitteri</i> (Bell), p. 429 |
| 5' | Marginal groove of pronotum nearly complete, ended short distance from anterior margin of pronotum; eyes more or less reduced..... | 6 |
| 6 (5') | Head evenly rounded posteriorly, widest point just posterior to eye; eye only moderately reduced, with about 100 ommatidia, deeper than long (Fig. 77) | <i>Yamatosa draco</i> (Bell), p. 429 |
| 6' | Head broadened posteriorly, widest point far posterior to eye; eye markedly reduced, with about 50 ommatidia, longer than deep (Fig. 85) | <i>Yamatosa boysi</i> (Arrow), p. 430 |

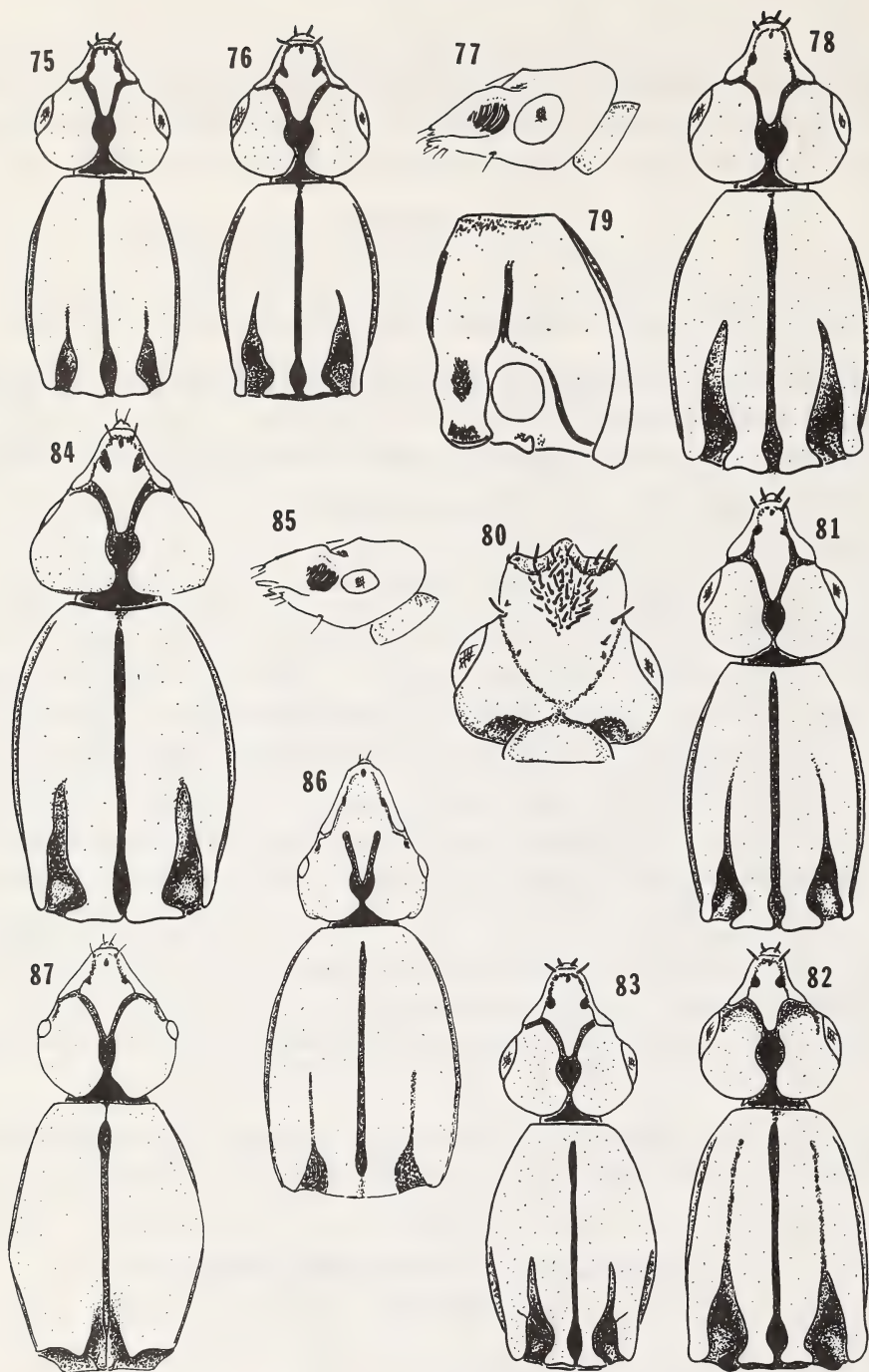
Yamatosa longior (Grouvelle 1903) NEW COMBINATION

Fig. 78-80)

Rhysodes niponensis var. *longior* Grouvelle 1903: 107.

Yamatosa longior (Bell and Bell) 1978.

Type material. – LECTOTYPE (here designated) female, labelled: “JAVA:Tougou, 3-96, coll. J.D. Pasteur” (MNHN). Two PARALECTOTYPES: one female, same data as lectotype (MNHN); one female, same data as lectotype, except that locality is spelled “Toegoe”, in Dutch orthography (LEI).



Figures 75 – 87. Fig. 75-85, Genus *Yamatosia*; Fig. 75-76, Head and pronotum, dorsal aspect; Fig. 75, *Y. peninsularis* (Arrow); Fig. 76, *Y. draco* Bell; Fig. 77, Head, lateral aspect, *Y. draco* Bell; Fig. 78-80, *Y. longior* (Grouvelle); Fig. 78. Head and pronotum, dorsal aspect; Fig. 79, Prothorax, ventrolateral aspect; Fig. 80. Head, ventral aspect; Fig. 81-84, Head and pronotum, dorsal aspect; Fig. 81, *Y. niponensis* (Lewis); Fig. 82, *Y. arrowi* (Grouvelle); Fig. 83, *Y. reitteri* Bell; Fig. 84, *Y. boysi* (Arrow); Fig. 85, Head, lateral aspect, *Y. boysi* (Arrow); Fig. 86,87, Head and pronotum, dorsal aspect; Fig. 86, *Shyrodes dohertyi* Grouvelle; Fig. 87. *Srimara planicollis* Bell and Bell.

Description. — Length 5.3–6.9 mm. Antennal Segment XI with apical stylet distinct; head cordate, anterior tentorial pits small, punctiform; frontal grooves narrow, well defined; eye large, deeper than long; mentum bearded in both sexes (Fig. 80); one pair of postlabial setae in most specimens.

Pronotum of medium length for the genus, length/greatest width about 1.33; base moderately narrowed; apex more strongly so; discal striole extended approximately to middle of pronotum; marginal groove complete; precoxal carina markedly developed, extended almost to anterior margin of prosternum (Fig. 79).

Strial punctures relatively fine; intervals relatively flat; Striae II, III abbreviated at base; Stria V effaced in basal sixth, only slightly impressed; Stria VI not impressed, absent in basal third, represented by row of minute punctures in apical two-thirds; Stria VII effaced in basal half, represented by minute punctures in apical half; elytral setae confined to apex of Stria VII.

Abdominal Sternum IV with very small lateral pits; Sternum V without pits; male with shallow oval median impression extended from middle of metasternum to abdominal Sternum III.

Anterior femur with ventral tooth in both sexes; anterior tibia of male with medial groove, latter bounded both anteriorly and posteriorly near base by pair of flanges; spurs of middle and hind tibiae nearly equal; hind calcar with tip just above level of spurs.

Although this species was described as a “variety” or subspecies of *Y. niponensis*, it is actually a distinct species, more like *Y. peninsularis* than like *Y. niponensis*. Contrary to Grouvelle’s key, it is not more elongate than *Y. niponensis*. The complete precoxal carinae separates *Y. longior* from all other members of the genus.

Range. — Java and Sumatra. In addition to the type material, we have seen the following specimens: JAVA: one female, Kopeng, 1600 m., 14-5-1933, coll. P.H.v. Doesburg (LEI); two males, Malang (MNH); one female, Mt. Tengge (MNH); one male, one female, G. Papandajan, 3-1916, coll. Drescher (AMS); one male, one female, Preanger, coll. P.F. Sijthoff (LEI); SUMATRA: one male, two females, Pajakombo (MNH).

Yamatosa peninsularis (Arrow 1942) NEW COMBINATION

(Fig. 75)

Rhysodes peninsularis Arrow 1942: 178.

Yamatosa peninsularis (Bell and Bell) 1978.

Type material. — HOLOTYPE male, labelled: “FEDERATED MALAY STATES: PAHANG: Tanak Rata, 4800 ft., Cameron’s Highlands, May 28, 1931, coll. H.M. Pendlebury” (BMNH).

Description. — Length 5.2 mm. Antennal Segment XI with distinct stylet; head cordate; anterior tentorial pits small, punctiform; frontal grooves narrow, well defined; eyes large, deeper than long; mentum bearded in male, beard less extensive than in *Y. longior*; status in female unknown; one pair of postlabial setae.

Pronotum longer and narrower than in *Y. longior*, length/greatest width 1.40; base moderately narrowed; apex markedly so; discal striole short, not extending beyond basal third of pronotum; marginal groove complete; precoxal carina present, shorter than in *Y. longior*, extended less than half the distance from coxa to anterior margin of pronotum.

Strial punctures relatively fine; intervals relatively flat; Striae II, III abbreviated at base; Stria V effaced in basal sixth, only slightly impressed; Stria VI not impressed, absent in basal third, represented by row of minute punctures in apical two-thirds; Stria VII effaced in basal half, represented by minute punctures in apical half; elytral setae confined to apex of Stria VII.

Abdominal Sternum IV of male with lateral pit larger than *Y. longior* (female unknown); Sternum V without lateral pits; holotype with raised tubercle in middle of metasternum (possibly an abnormality), metasternum not as definitely impressed at middle as in *Y. longior*.

Anterior leg of male as in *Y. longior*; spurs of middle and hind tibiae nearly equal; hind calcar larger than in *Y. longior*, with upper oblique margin longer.

This species is easily identified by the half-length precoxal carina. It also differs from *Y. longior* in having a more elongate pronotum with notably small basal impressions and shorter discal striae.

Yamatosa niponensis (Lewis 1888) NEW COMBINATION

(Fig. 81)

Rhysodes niponensis Lewis 1888: 82.

Yamatosa niponensis Bell and Bell 1978

Type material. — LECTOTYPE (here designated) male, labelled: "JAPAN: Honshu, Hakone District, coll. G. Lewis" (BMNH). Six PARALECTOTYPES: one male, two females, same data as lectotype (BMNH); one female, JAPAN: Subushri (BMNH); one male, one female (no specific locality), coll. G. Lewis, 1910-320, C.F. Baker Colln. (1927) (NMNH). The male is labelled as a "co-type".

Description. — Length 5.4–7.0 mm. Antennal Segment XI with apical stylet distinct, though small; head cordate, anterior tentorial pits small, punctiform; frontal grooves narrow, well-defined; eye large, deeper than long; mentum conspicuously punctate and bearded in male; in female beard greatly reduced to absent, punctures very fine; one pair of postlabial setae.

Pronotum moderately elongate for genus, length/greatest width about 1.40; base moderately narrowed; apex more strongly narrowed; discal striole extended 0.66 length of pronotum; marginal groove complete; precoxal carina absent; a group of many punctures anterior to each front coxa.

Strial punctures fine, intervals relatively convex; Striae II, III scarcely abbreviated at base; Stria V slightly abbreviated at base, only shallowly impressed, coarsely punctate; Stria VI not impressed, represented by row of fine punctures; Stria VII represented by minute punctures in anterior half; those of posterior half coarser; only apex of Stria VII impressed; elytral setae confined to apex of Stria VII.

Abdominal Sternum IV with lateral pits; Sternum V without pits; metasternum shallowly impressed medially in male.

Anterior femur with ventral tooth in both sexes; anterior tibia of male slightly swollen near base, with trace of groove on medial surface (much less distinct than in preceding species); spurs of middle and hind tibiae nearly equal; hind calcar of male small, forming subacute angle immediately above spurs.

This species resembles *Y. peninsularis* in form, but differs from the latter in the complete absence of a precoxal carina, and in the much less distinct medial groove on the anterior tibia.

Range. — Japan and Taiwan. A series in MNHN, labelled: "Sydney, Australia", is surely mislabelled, as the genus is otherwise unknown east of Java. In addition to the type material, we have seen the following specimens: JAPAN: (HOKKAIDO) one female, Wakoto, 5-VII-1958, coll. F. Takechi (SATO); (HONSHU) one female, Hida, VII, 1957, coll. H. Torigai (SATO); one female, Hida, Futatsuya, VI-1954, coll. H. Torigai (SATO); one female, Hida, Idani, Kawai, VII-1953, coll. H. Torigai (SATO); Ikenoshima, 900' (Higashimata, Nikko District) (sex and number not recorded) (BMNH); two males, Tsuta-yu (Towada), VII-25-1954, coll. J. Aoki (DY); (KYUSHU) one male, one female, Mt. Homan, Fukuoka, 7-IV-1965, coll. M.T. Chuyo (MNHB); Nagasaki, Chiuzenji, Ichiuchi, Oyayama District (numbers and sexes not recorded) (BMNH); (SHIKOKU) one male, one female, Mt. Kohtsu (Tokushima), 31-X-1965, coll. M. Sakai (SATO); one female, Omogo, 10-VII-1956, coll. M. Satô (SATO). TAIWAN (FORMOSA): one male, Taiheizan, 6-V-1932, coll. L. Gressitt (CAS).

According to Lewis, this species is found under the bark of firs (*Pinus*) (now in the genus *Abies*).

Yamatosa arrowi (Grouvelle 1908) NEW COMBINATION
(Fig. 82)

Rhysodes arrowi Grouvelle 1908: 318.

Yamatoa arrowi Bell and Bell 1978.

Type material. — HOLOTYPE female, labelled: "SIKKIM" (MNHN).

Description. — Length 9.5 mm. Antennal Segment XI with distinct stubby stylet; head cordate; anterior tentorial pits large, rounded; frontal and antennal grooves dilated, their posterior margins indistinctly defined; eye large, deeper than long; mentum punctate and bearded in female (male unknown); two pairs of postlabial setae.

Pronotum moderately elongate; length/greatest width 1.38; apex markedly narrowed; base much less narrowed than in other members of the genus; discal striole 80% of length of pronotum; marginal groove complete; precoxal carina and precoxal punctures absent.

Strial punctures relatively coarse; elytral setae limited to apex of Stria VII; abdominal Sternum IV with distinct lateral pits; Sternum V without lateral pits.

Anterior femur with large acute ventral tooth in female (male unknown); spurs of middle and hind tibiae nearly equal.

Enlarged anterior tentorial pits, dilated frontal grooves, broad base of the pronotum, and very long discal striae are diagnostic of this species, which is also much larger than other members of the genus.

Yamatosa reitteri (Bell 1977) NEW COMBINATION
(Fig. 83)

Rhysodes boysi auct., nec. Arrow

Yamatosa reitteri (Bell), 1977: 152.

Type material. – HOLOTYPE male, labelled; “INDIA, U. Gumti Val. W. Almora Dn., Apr. 19, coll. H. Gower Champion” (BMNH). 14 PARATYPES, listed in Bell (1977), 7 (BMNH), 4(MNHN), 3(BSL).

Description. – Length 6.2–7.3 mm. Antennal Segment XI obtuse, stylet absent; head cordate, sides evenly rounded; anterior tentorial pits, rounded; frontal grooves narrow, well defined; eye large, deep, with more than 150 ommatidia; mentum nearly smooth, without beard; one pair of postlabial setae.

Pronotum moderately long for the genus, length/greatest width 1.37; base moderately narrowed, apex more strongly narrowed; discal striae ending anteriorly at basal third of pronotum; marginal groove largely effaced, distinct only in basal fourth of pronotum; precoxal carina absent; precoxal punctures absent.

Elytra relatively elongate, narrow; humeral tubercle relatively prominent in form of small, laterally-directed tooth; striae punctures relatively coarse; intervals moderately convex; Striae II, III abbreviated at base; Stria V slightly impressed, its anterior end slightly posterior to humeral tubercle; Stria VI only slightly abbreviated anteriorly; elytral setae confined to apex of Stria VII; hind wings fully developed.

Male with neither metasternum nor abdomen concave; Sternite IV (both sexes), with conspicuous lateral pits, shallower in male; Sternite V with smaller, shallower lateral pits.

Anterior femur without ventral tooth in either sex; anterior tibia of male without medial groove or swelling; anterior spur conspicuously smaller than posterior one on both middle and hind tibiae; hind calcar of male in form of small acute angle immediately above level of spurs.

The male genitalia were figured in Part I, 68.

This species differs from all others in the genus in having the marginal grooves of the pronotum largely effaced.

Y. reitteri is confined to the middle and eastern Himalaya, from Kumaon District to Bhutan. It is not known from Himachal Pradesh or Kashmir. Bell (1977) gives a list of localities.

Yamatosa draco (Bell 1977) NEW COMBINATION
(Fig. 76,77)

Yamatosa draco Bell 1977: 155

Type material. – HOLOTYPE male, labelled; “BHUTAN: Tango, 12 kilometers north of Thimphu, 2500-2900 m. June 30, 1972, coll. Basel Natural History Museum Expedition” (BSL).

Description. – Length 6.7 mm. Antennal Segment XI obtuse; stylet absent; head cordate, sides evenly rounded, widest point opposite middle of temporal lobe, just posterior to eyes; anterior tentorial pits small, oblique; frontal grooves very narrow, clearly defined; eye reduced (Fig. 77), deeper than long, entirely anterior to middle of temporal lobe, with about 100 ommatidia; cornea distinctly faceted; mentum nearly smooth, without beard; one pair of postlabial setae.

Pronotum relatively short for genus, length/greatest width 1.33; base distinctly narrowed; apex more strongly narrowed; discal striae ended anteriorly at basal third of pronotum; marginal groove nearly complete, effaced only near anterior end of pronotum; precoxal carina absent; precoxal punctures absent.

Elytra relatively short, broad for genus; humeral tubercle small; striae punctures small but deep; Striae II, III slightly abbreviated at base; Stria V represented only by row of punctures in anterior half; slightly impressed in posterior half; Stria V with origin slightly posterior to humerus; Stria VI only slightly abbreviated anteriorly; Striae II and IV each with one seta near apex; several setae also in apex of Stria VII; status of hind wings not investigated.

Male with metasternum broadly concave, abdominal sterna not concave; Sternum IV with deep lateral pits; Sternum V with shallow ones; lateral pits suggested on Sternum III.

Anterior femur of male with ventral tooth (female unknown); anterior tibia of male without medial groove or swelling; spurs of middle tibiae unequal, anterior ones smaller; spurs of hind tibiae equal; calcar small, obtusely angled.

This species is closely related to the allopatric *Y. boysi*, with which it agrees in having reduced eyes, oblique anterior tentorial pits, and setae in elytral Striae II and IV. This species has the eyes much less reduced and the shape of the head less modified than in *Y. boysi*. Size and shape are similar to those of

the sympatric *Y. reitteri*, but the latter species has reduced marginal grooves on the pronotum, and eyes which are not reduced.

Yamatosa boysi (Arrow 1901) NEW COMBINATION

(Fig. 84, 85)

Rhysodes boysi Arrow 1901: 87.

Rhysodes kaschmirensis Reitter 1922: 57.

Yamatoa boysi Bell and Bell 1978.

Type material. — *R. boysi*: LECTOTYPE (here designated) female, labelled: "INDIA: 1901-58, coll. Capt. Boys" (BMNH). PARALECTOTYPE: the original description states that there were two females in the type series. We were unable to locate the second female. If it still exists, it constitutes a paralectotype.

R. kaschmirensis: A series of four specimens in Paris (MMHN) are labelled: "Kaschmir, Reitter". One of these bears a determination in the same handwriting "*R. kaschmirensis* Reitter". It is our belief that these specimens are cotypes.

Description. — Length 6.0–7.2 mm. Antennal Segment XI obtuse; stylet absent; head inflated, distinctly broader than long, widest point at basal fourth, far behind eyes; anterior tentorial pits small, oblique; frontal grooves narrow, well defined; eye markedly reduced (Fig. 85), longer than wide, rounded anteriorly, angled posteriorly, extended only 0.33 of distance from antennal base to rear of temporal lobe, only 0.25 of depth of head; eye flat, cornea not faceted; about 50 ommatidia; mentum nearly smooth, without beard; one pair of postlabial setae.

Pronotum moderately short for genus, length/greatest width about 1.38; base distinctly narrowed; apex more markedly narrowed; discal striae ended anteriorly at basal third of pronotum; marginal groove nearly complete, effaced only near anterior end of pronotum; precoxal carina absent; precoxal punctures absent.

Elytra short and broad for genus; humeral tubercle small; striae punctures coarse; Striae II, III slightly abbreviated at base; Stria V originating slightly posterior to humerus, its anterior half represented by a row of punctures, its posterior half slightly impressed; Stria VI only slightly abbreviated anteriorly; Striae II and IV each with apical seta (one or the other missing in some specimens); several setae also present in apex of Stria VII; hind wings reduced to small vestiges.

Male with metasternum broadly, shallowly concave; abdominal sterna not concave; metasternum of female evenly convex; Sternite IV with deep lateral pits; Sternite V with shallow ones.

Anterior femur of male with ventral tooth; that of female without tooth; anterior tibia of male without medial groove or swelling; spurs of middle and posterior tibiae nearly equal; hind calcar of male shaped as in *Y. draco*, but distinctly larger. The male genitalia have been figured by Saha, Mukherjee and Sengupta (1978).

Inflated, somewhat wedge-shaped head and strongly reduced eyes give this species a distinctive appearance. It is the only species of *Yamatosa* in which the sexes are known to differ in development of the femoral tooth. (In *Y. draco*, however, the female is unknown.)

Range. — As presently known, almost entirely to the west of that of *Y. reitteri*, the two species occurring together only in Kumaon. The range of *Y. boysi* extends westward along the Himalaya to the Indus River in the Pakistani part of Kashmir. We have seen specimens from the following localities: INDIA: two males, Chakrata Div. U.P., 7000 ft., I-VII-1932, coll. H.G. Champion (BMNH); four males, two females, Chapal, Himachal Pradesh, 2400-2750 m, 7-5-1977, coll. W. Wittmer, Brancucci (BSL); one male, Dudhatoli, Garhwal, 9000 ft., June 1920, coll. H.G. Champion (BMNH); one female, Gori Valley, Kumaon, no date, 7000 ft., coll. H.G. Champion (BMNH); one female, Parbatti V., Kulu, Punjab, 6000-8000 ft., no date, coll. H.G. Champion (BMNH); KASHMIR: one female, Chhangla Gali, 7000 ft. Hazara, 12-VI-1974, coll. C. Baroni Urbani (BSL); one male, three females, Gulmarg, 16-VII-31, Fletcher colln. (BMNH); one male, one female, Yusmarg, 2300-2400 m., 5-7-1976, coll. W. Wittmer (BSL).

In addition, nine other specimens which we have not seen have been reported by Saha, Mukherjee and Sengupta (1978) from Himachal Pradesh as follows: three males, four females, Bagi, 2518 m., 21-VI-1975; one male, one female, Narkanda, 2725 m., 20-VI-1975, all collected by T. Sengupta.

Genus *Shyrodes* Grouvelle 1903

Type species. – *Rhysodes dohertyi* Grouvelle 1903.

Description. – Part I, 69. Only one species is known.

Shyrodes dohertyi (Grouvelle 1903)
(Fig. 86)

Rhysodes dohertyi Grouvelle 1903: 126.

Description. – Part I, 69.

Type material. – Part I, 69.

The name of the country of origin, BURMA, was inadvertently omitted from Part I. “Ruby Mines”, the type locality, refers to the vicinity of Mogok, about 140 km north of Mandalay. A Doherty specimen in the MCZ collection has additional collecting data of 5000-7000 feet.

Genus *Srimara* Bell & Bell 1978

Type species. – *Srimara planicollis* Bell & Bell 1978.

Description. – Part I, 70.

Type material. – Part I, 70. Only one species is known.

Srimara planicollis Bell & Bell 1978
(Fig. 87)

Srimara planicollis Bell & Bell 1978: 70.

Description. – Part I, 70.

Type material. – Part I, 70.

Genus *Plesioglymmius* Bell and Bell 1978
(Fig. 88-102)

Type species. – *Rhysodes elegans* Grouvelle 1903.

Description. – Segment IX of antenna varied from sharply pointed to obtuse; minor setae on Segments V-X; basal setae present or absent; antennal bases more or less displaced dorsomedially; clypeus separated from median lobe by transverse impression, latter ill-defined or very deep and distinct; or else clypeus and median lobe broadly separated by junction of antennal sclerites in midline; clypeal setae present or absent; eyes fully developed, with distinct ommatidia.

Pronotum with paramedian grooves incomplete anteriorly, in most species paramedian grooves broad, in form of paramedian grooves characteristic of *Omoglymmius* except not extended to reach anterior margin; in subgenus *Juxtaglymmius*, anterior portions of paramedian grooves in form of discal striae as in *Yamatosa*; marginal grooves fine, complete.

Elytral setae virtually constant within genus; Stria II with one to four in apex; Stria IV with many setae in form of complete series; one seta on apical tubercle; one to three setae in apical stria; several setae in tip of Stria VII; hind wings long; middle and hind tibiae each with one spur.

The above description has been modified from the original one (Part I, 70–71) to accommodate *Plesioglymmius* (*Juxtaglymmius*) *jugatus*. The latter species has the paramedian grooves reduced to discal striae, much as in *Yamatosa*. Nevertheless, loss of inner spurs of the middle and hind tibiae and tendency for the antennal bases to approach one another seem to indicate that *P. jugatus* is a modified

Plesioglymmius and not a relative of *Yamatosa*.

Plesioglymmius is found in two widely disjunct areas: the Greater Sunda Islands (Sumatra, Borneo, Java and Mindanao), and Latin America (Brazil, Venezuela, and perhaps Cuba). The three subgenera are clearly distinct, and there is no decisive evidence to indicate that any two of them are more closely related than either is to the third.

Although there are six distinct species, the genus is known from less than 20 specimens. This makes it excessively rare, even among *Rhysodini*, and suggests that it is limited to some special and inaccessible habitat.

KEY TO SUBGENERA

- 1 Antennal sclerites separated from one another (Fig. 88); paramedian groove not linear, extending about 90% of distance from base to apex of pronotum 2
- 1' Antennal sclerites joined as median suture between clypeus and median lobe, latter thus separated (Fig. 89); paramedian groove linear, in form of discal striole, ended near middle of pronotum *Juxtaglymmius* new subgenus, p. 437
- 2 (1) Paramedian grooves coarsely punctate, glabrous except for pollinosity in punctures; medial angles of temporal lobes distinct; median lobe of head rhomboid *Ameroglymmius* new subgenus, p. 435
- 2' Paramedian grooves entirely pilose, without visible punctures; medial margin of temporal lobe truncate, without distinct medial angle; median head lobe oval *Plesioglymmius (sensu stricto)* Bell and Bell, p. 432

Subgenus *Plesioglymmius (sensu stricto)* Bell and Bell 1978

Type species. – *Rhysodes elegans* Grouvelle 1903

Description. – Antennal Segment XI longer than wide; stylet short; Segments I, II pollinose dorsally; Segments III-IV each with narrow subapical dorsal pollinose band; basal setae present on Segments V-X.

Clypeus concave, with pair of setae; median lobe of head oval, isolated from clypeus by deep transverse pilose impression, latter bounded anteriorly by raised, pollinose posterior margin of clypeus; antennal sclerites widely separated from one another; medial margin of temporal lobes truncate, the two temporal lobes thus separated by narrow linear space; one or more coarse punctures near medial margin of each temporal lobe; orbital groove represented by strip of pollinosity; temporal setae present or absent; postorbit evenly convex; postorbital tubercle absent; suborbital tubercles prominent, in form of posterior ends of distinct genal ridges; much of ventral surface of head, including genal ridges pilose; two to four pairs of postlabial setae.

Paramedian grooves deep, straight, about 95% as long as pronotum; both median and paramedian grooves coarsely punctate, but with punctures almost completely concealed by coarse pilosity; pleural regions impunctate.

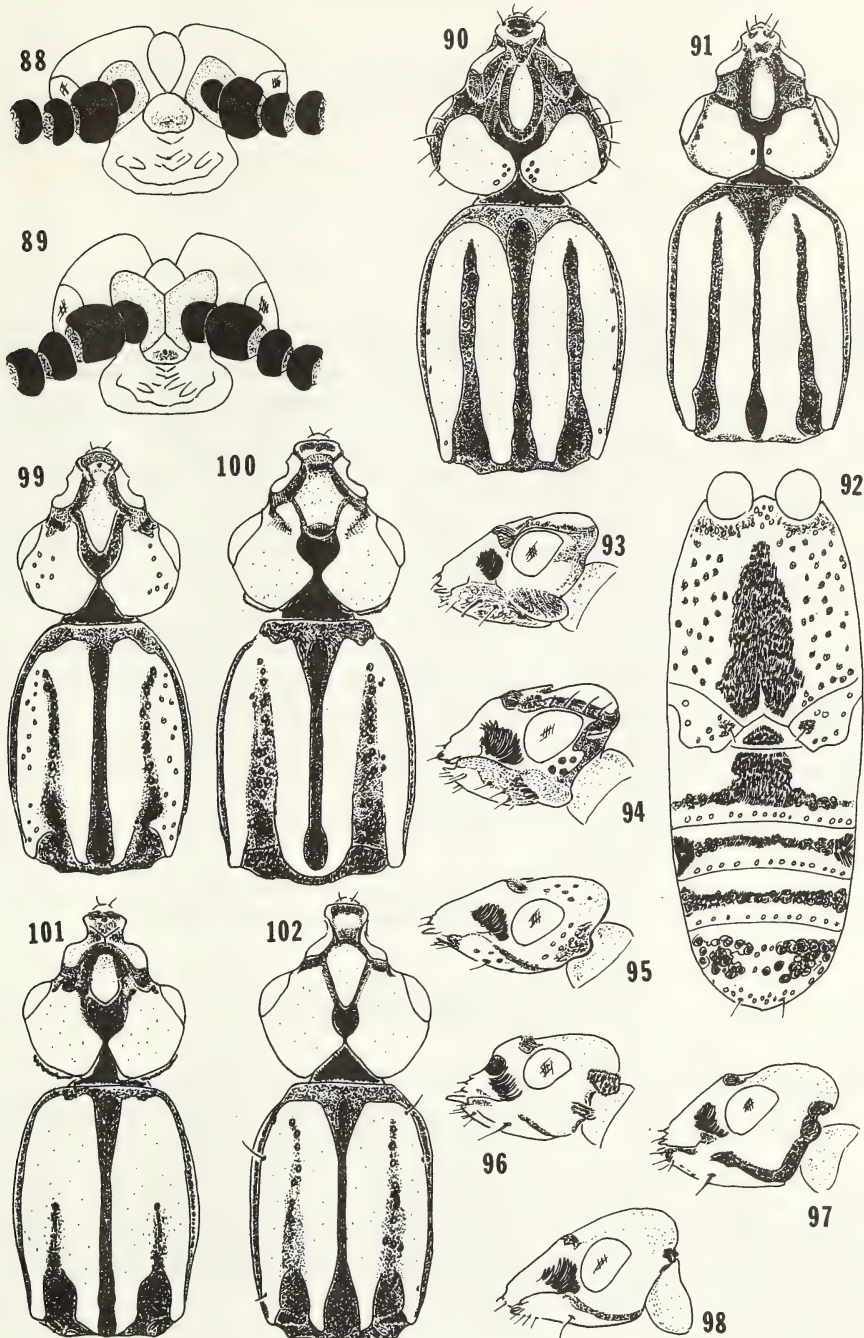
Base of elytron opposite Interval I extended anteriorly in form of angulate tooth; elytral striae deep; striae punctures coarse; apical depression of elytron including tips of Striae I, IV; medial margin of apical tubercle distinctly sinuate.

The truncate medial margin of the temporal lobe is unique to this subgenus. It also differs from other subgenera of *Plesioglymmius* in having the paramedian grooves straight, and entirely pollinose.

The subgenus *Plesioglymmius (sensu stricto)* is known from Sumatra, Borneo, and Mindanao.

KEY TO SPECIES

- 1 Temporal setae absent; orbital groove represented by narrow strip of pollinosity; postorbit without a seta *Plesioglymmius elegans* (Grouvelle), p. 434



Figures 88 – 102. Genus *Plesioglymmius*. Fig. 88,89, Head, anterior aspect, semi-diagrammatic, antennal segments, black; antennal sclerites, stippled; Fig. 88, *P. (Plesioglymmius) silus* new species; Fig. 89, *P. (Juxtaglymmius) jugatus* new species; Fig. 90, Head and pronotum, dorsal aspect, *P. (P.) silus*, new species; Fig. 91-93, *P. (P.) elegans* (Grouvelle); Fig. 91, Head and pronotum, dorsal aspect; Fig. 92, Metasternum and abdomen, ventral aspect, male; Fig. 93, Head, male, lateral aspect; Fig. 94-98, Head lateral aspect; Fig. 94, *P. (P.) silus* new species; Fig. 95, *P. (Ameroglymmius) meridionalis* (Grouvelle); Fig. 96, *P. (J.) jugatus* new species; Fig. 97, *P. (A.) reichardti* new species; Fig. 98, *P. (A.) compactus* new species; Fig. 99-102, Head and pronotum, dorsal aspect; Fig. 99, *P. (A.) meridionalis* (Grouvelle); Fig. 100, *P. (A.) reichardti* new species; Fig. 101, *P. (J.) jugatus* new species; Fig. 102, *P. (A.) compactus* new species.

- 1' Four to five temporal setae present; orbital groove represented by broad strip of pollinosity; postorbit with a seta..... *Plesioglymmius silus* new species, p. 434

Plesioglymmius (sensu stricto) elegans (Grouvelle 1903)
(Fig. 91-93)

Rhysodes elegans Grouvelle 1903: 117-118

Type material. – LECTOTYPE (here designated) male, labelled; “SUMATRA, Palembang” (MNHN). Three PARALECTOTYPES: two males, one female, same data as lectotype (MNHN).

Description. – Length 4.3–5.5 mm. Head slightly longer than broad; antennal stylet short, acute; clypeus less constricted posteriorly than in *P. silus*, its base only moderately raised; temporal lobe with one to two punctures near medial margin; temporal setae absent; orbital groove represented by very narrow pollinose strip, latter with small tufts of pollinosity; postorbit pollinose, impunctate; postorbital seta absent (Fig. 93); mentum entirely pollinose except anterior margin in male, pollinosity limited to medial area of mentum and genae in female; one to two pairs of postlabial setae.

Pronotum elongate, length/greatest width about 1.45; pronotum hexagonal, sides straight, nearly parallel, apex and base both abruptly narrow, each forming a distinct angle with remainder of lateral margin; median groove narrow, linear near middle; paramedian grooves relatively narrow; pronotal carinae impunctate; in male, prosternum pilose except for small area anterior to each coxa; in female, prosternum finely pollinose in anterior fourth, remainder coarsely punctate.

Each elytral stria with fine strip of pollinosity connecting punctures; metasternum of male with median pilose area extended from slightly posterior to middle coxal cavities to posterior margin; sides of metasternum coarsely punctate; in female, metasternum glabrous, median area with few scattered punctures, lateral regions coarsely punctate; pollinosity of male extended onto medial portion of hind coxae and abdominal Sterna I, II, ending abruptly at anterior transverse row of punctures on Sternum III (Fig. 92); female without pilosity on hind coxae or abdominal Sterna I, II; in both sexes, Sterna II-V each with two transverse rows of punctures, those of anterior row very coarse, surrounded by pollinosity, more or less coalescent into transverse pollinose strip; punctures of posterior row much finer, not surrounded by pollinosity; both sexes with distinct lateral pits in Sternum IV; male with ventral tooth on anterior femur; middle and hind calcaria both small, acute.

Absence of temporal setae, and hexagonal form of the pronotum are among several striking differences between this species and *P. silus*.

Range. – Sumatra and Borneo. In addition to the type material, we have seen one male, labelled: “BORNEO: S. East; German Mission 59773, Fry Collection 1905. 100” (BMNH).

Plesioglymmius (sensu stricto) silus new species
(Fig. 88,90,94)

Type material. – HOLOTYPE female, labelled; “PHILIPPINES: Kabasalan, Zamboanga, Mindanao, VIII-1932, coll. H.G. Muzzell” (CAS). PARATYPES two females, same data as type (CAS).

Description. – Length 6.0–6.9 mm. Head shorter and broader than in *P. elegans*, clearly broader than long; antennal stylet short, blunt; clypeus more markedly constricted at base than in *P. elegans*, its base strongly raised; temporal lobe with cluster of two to five coarse punctures near medial margin; four to five prominent temporal setae present, inserted within broad strip of pollinosity which represents orbital groove; postorbit finely pollinose, with distinct coarse punctures; postorbit with one prominent seta opposite upper fourth of eye (Fig. 94); mentum largely glabrous, contrasting with pollinose genal ridges; four pairs of postlabial setae.

Pronotum shorter than in *P. elegans*, length/greatest width is 1.36; widest point anterior to middle, sides curved; apex markedly narrowed; base moderately narrowed; median groove broader than in *P. elegans*; paramedian grooves slightly broader than in *P. elegans*; outer carina with few coarse punctures near lateral margin, and many very fine, scattered punctures; prosternum of female extensively pollinose anteriorly, pollinosity extended to coxal cavities laterally; posterior half of prosternum glabrous, coarsely punctate (male unknown).

Elytra with stria punctures not connected by pollinosity; metasternum of female entirely coarsely punctate, not pollinose (male unknown); abdominal Sterna III-V each with two transverse rows of punctures; anterior rows coarse, surrounded by pollinosity, latter more or less coalescent in form of transverse pollinose bands; posterior rows fine, without pollinosity; female with distinct lateral pits in abdominal Sternum IV (male unknown).

This species has a shorter, broader head than does *P. elegans*, and is easily recognized by the presence of temporal setae.

Subgenus *Ameroglymmius* new subgenus

Type species. – *Rhysodes meridionalis* Grouvelle 1903

Description. – Antennal Segment XI either elongated, conical or shorter, obtuse; basal setae present on Segments V-X, or limited to Segments VIII-X, or entirely absent; Segment I pollinose dorsally; remaining segments either with small pollinose spots at bases of basal setae, or else entirely without pollinosity; clypeus flat, without setae; median lobe of head rhomboidal; transverse groove between clypeus and median lobe either shallow and indefinite or deep and distinct; antennal sclerites widely separated; medial margin of temporal lobe angulate, the medial angles contiguous or narrowly separated; orbital groove and temporal setae absent; postorbital tubercle present; suborbital tubercle and genal ridges absent; lower surface of head glabrous except for gular grooves; one pair of postlabial setae.

Paramedian grooves deep, broad, gradually tapered anteriorly, extended about 95% of length of pronotum; paramedian grooves at least slightly sinuate, their anterior ends slightly divergent; paramedian grooves coarsely punctate, without pollinosity except within punctures.

Base of elytron opposite Interval I either in form of rounded prominence or else not projected; elytral striae shallow or not impressed; striae punctures coarse; no pollinosity between punctures; apical depression limited to apices of Striae I and II; apical tubercle not sinuate medially; metasternum coarsely punctate; abdominal punctures not in rows, but irregularly distributed; lateral pits on Sternum IV of female, absent from male.

The coarsely punctate paramedian grooves and the rhomboidal median lobe are diagnostic of this subgenus. It is found in eastern South America, and possibly in Cuba.

Phylogeny. – *P. meridionalis* stands apart from the other two species in having a relatively long head, lateral eyes, antennal bases far apart, and frontal grooves relatively broad. In all these features, it is the least specialized species of *Plesioglymmius*. *P. reichardti* and *P. compactus* have the head shortened, eyes directed anterolaterally, frontal grooves linear, and antennal bases relatively close together; antennal apex obtuse, and basal setae of the antenna reduced.

KEY TO SPECIES

- | | | | |
|-------|--|--|-----|
| 1 | Antennal Segment XI acutely pointed; frontal grooves relatively broad; outer carina of pronotum coarsely punctate | <i>Plesioglymmius meridionalis</i> (Grouvelle), p. | 435 |
| 1' | Antennal Segment XI obtuse; frontal grooves linear; outer carina impunctate or with few small punctures | | 2 |
| 2 (1) | Median lobe truncate posteriorly at level of anterior margin of eye; marginal setae absent; anterior and posterior median pits of pronotum deep, expanded | | |
| | | <i>Plesioglymmius reichardti</i> new species, p. | 436 |
| 2' | Median lobe obtusely pointed posteriorly at level of posterior margin of eye; marginal setae present; anterior and posterior median pits of pronotum shallow | | |
| | | <i>Plesioglymmius compactus</i> new species, p. | 437 |

Plesioglymmius (*Ameroglymmius*) *meridionalis* (Grouvelle) NEW COMBINATION (Fig. 95, 99)

Rhysodes meridionalis Grouvelle 1903: 108–109

Type material. – LECTOTYPE (here designated) male, labelled: "Brasilia" (MNHN). PARALECTOTYPES one male, labelled: "Brazilia, co-type, Fry Coll. 1905-100" (BMNH); one female, labelled: "Rio San°, co-type, Fry. Coll. 1905-100" (BMNH).

Description. – Length 5.2-6.7 mm. Antennal Segment XI longer than wide, its apex bluntly pointed, suggesting vestigial stylet; basal setae on Segments V-X; Segment I pollinose dorsally with deeper pilose punctures; Segments II-VI with shallow pollinose punctures.

Head slightly longer than broad; eyes completely lateral; antennal sclerites relatively widely separated; transverse groove between clypeus and median lobe shallow, incompletely pollinose, in some specimens apparently interrupted in midline; median lobe small, obtuse to nearly acute; median lobe with apex opposite middle of eye; frontal grooves broad; medial angles obtuse, slightly separated; temporal lobes coarsely, sparsely, irregularly punctate; postorbit with two irregular vertical rows of coarse punctures posterior to eye, very finely pollinose posterior to the punctures; postorbital tubercle distinct, but postorbit very shallowly emarginate dorsal to it (Fig. 95); mentum coarsely punctate, pollinosity of gular grooves incomplete.

Pronotum narrow, rather elongate, widest at posterior third; sides curved, base distinctly narrowed, apex more strongly so; paramedian groove coarsely punctate; marginal groove more dilated than in related species; marginal setae absent; inner carina impunctate; outer carina coarsely, irregularly punctate; epipleura and prosternum coarsely punctate.

Basal scarp of elytron transverse except for rounded prominence opposite base of Stria I; both sexes with prominent ventral tooth on anterior femur, and obtuse one on hind femur. Male with middle calcar acute, triangular; hind calcar obtuse.

The coarsely punctate outer carinae and temporal lobes distinguish this species. It can be separated from *P. reichardti* also by the pointed median lobe and the more elongate head.

Distribution. – Southern Brazil. In addition to the type material, we have seen the following specimens: one male, one female, Cantaneira (San Paulo State), 20-II-1958, coll. K. Lenko (MZSP); one female, Nova Teutonia (Santa Catarina State), XI-1940, 300-500 m., coll. Fritz Plaumann (MZSP); one female, Brazil, Paraná, 1901-31, coll. G. Lewis (BMNH); one female, Represa do Cabeca, Corcovado (Rio, D.F.), 27-7-1967, coll. Wygodzinsky (MZSP).

Vulcano and Pereira (1975a) also list this species from Agua Funda, Alto da Serra and Paraná, Curitiba. We have not studied the specimens from these localities. Their record from Suapure, Venezuela actually pertains to *P. reichardti*. These specimens of *P. meridionalis* in the Carnegie Museum (CMP) are labelled: "Denver, Colorado, H. Klages coll." C.M. acc. 11414. According to G. Wallace, E.A. Klages, a brother of H. Klages, collected extensively in South America, and these are no doubt mislabelled Brazilian specimens.

Plesioglymmius (Ameroglymmius) reichardti new species
(Fig. 97,100)

Type material. – HOLOTYPE male, labelled: "VENEZUELA: Suapure, Caura R., Apr. 25, 1899, coll. E.A. Klages" (MZSP). PARATYPE female, labelled: "BRAZIL: Rio Madeira, Mann & Baker, W.M. Mann Coll. 1954" (MZSP).

Description. – Length 5.0-5.3 mm. Antennal Segment XI somewhat compressed, longer than wide, obtusely rounded at apex, stylet absent; basal setae absent from Segments V-VII, but present on VIII-X; antenna without pollinosity except for dorsal spot on Segment I.

Head wider than long; eyes directed slightly anteriorly and dorsally; antennal sclerites relatively narrowly separated; clypeus and median lobe separated by a deep, pollinose transverse groove; median lobe relatively short, broad, pentagonal, abruptly truncate at level of anterior margin of eye; frontal grooves linear; medial angles narrowly separated; temporal lobes apparently impunctate except at high magnification; postorbit pollinose, impunctate; postorbital tubercle distinct (Fig. 97); gular grooves occupied by broad, continuous bands of pollinosity.

Pronotum narrow, rather elongate, widest at posterior third, sides slightly curved to base, latter slightly narrowed, markedly curved to apex, latter markedly narrowed; paramedian grooves coarsely, rather densely punctate; basal impressions with rather long pilosity; marginal groove fine, shallow; marginal setae absent; both inner and outer carinae entirely impunctate; epipleura and propleuron impunctate; prosternum coarsely punctate.

Basal scarp of elytron transverse except for rounded prominence opposite Stria I; male with ventral tooth on anterior and posterior femora; female without femoral teeth; calcar of middle tibia acute; hind calcar small, narrow, its tip slightly upturned.

The markedly truncate median lobe is the recognition mark of *P. reichardti*. It also differs conspicuously from *P. meridionalis* in absence of punctures from the outer pronotal carinae and temporal lobes. This species is dedicated to the memory of Dr. Hans Reichardt, whose untimely death in

1976 was a great loss for the science of entomology. This species appears to be restricted to the Orinoco and Amazon Basins, and to be allopatric to *P. meridionalis*.

Plesioglymmius (Ameroglymmius) compactus new species
(Fig. 98,102)

Type material. – HOLOTYPE female, labelled: “CUBA” (MCZ).

Description. – Length 4.8 mm. Antennal Segment XI slightly longer than wide, cone tapered, its tip obtusely rounded, stylet absent; basal setae absent; Segment I pollinose above; remaining segments devoid of pollinosity.

Head wider than long; eyes directed slightly dorsally and anteriorly; antennal sclerites relatively close together; clypeus and median lobe separated by deep, pollinose transverse groove; clypeal setae absent; antennal sclerites relatively close together, median lobe rhomboidal, its tip obtusely pointed at level of posterior margin of eye; temporal lobes short, rather inflated; frontal grooves sublinear; medial angles obtusely rounded, contiguous; temporal lobes impunctate; postorbit glabrous, convex; postorbital tubercle minute, pollinose (Fig. 98); mentum with few median punctures; gular grooves occupied by broad, continuous bands of pollinosity.

Pronotum elongate, narrow, broadest clearly anterior to middle; sides almost straight, slightly convergent posteriorly; base and apex distinctly narrowed; paramedian grooves relatively narrowed; the punctures of each groove in form of a single irregular line; marginal groove fine, shallow; marginal setae present (some setae missing on holotype, but the punctures indicate two setae near apex and one near base on each side); both inner and outer carina impunctate; prosternum with broad, irregular band of coarse punctures on either side of midline, otherwise impunctate; proepipleura and propleuron both impunctate.

Elytral humerus narrow, triangular; basal scarp of elytron angled opposite base of Stria IV; no prominence opposite base of Stria I; striae not impressed, represented by rows of fine punctures; Striae II, III slightly abbreviated at base; female with distinct lateral pit on abdominal Sternum IV; male unknown.

This species is the only member of the genus to have marginal setae on the pronotum. The arrangement of the punctures of the paramedian groove in a single line is also unique. The holotype has the tip of one wing protruding between the elytra, as is often seen in Carabidae collected at lights. At first glance, the eyes of this species appear reduced, but this is an optical illusion caused by the shortening and inflation of the temporal lobes.

According to Dr. P.J. Darlington, Jr. (personal communication), this specimen was from the Blaisdell collection which contains many erroneous locality records. So perhaps, the specimen is not really from Cuba. If so, it would probably prove to be a South American species. Bell (1970) discussed but did not name this species.

Subgenus *Juxtaglymmius* new subgenus

Type species. – *Plesioglymmius (Juxtaglymmius) jugatus* new species

Description. – Antennal Segment XI longer than wide, acutely pointed in form of vestigial stylet or none; basal setae sparse, on Segments V-X; Segment I pollinose dorsally; Segment II with basal pollinose band, remaining segments without pollinosity; antennal sclerites meeting in contact in form of median suture, clypeus thus widely separated from median lobe; clypeus flat; clypeal setae absent; median lobe small, oval, markedly convex; medial angles of temporal lobes obtuse, narrowly separated; orbital groove and temporal setae absent; postorbital tubercle prominent, separated from temporal lobe by deep notch; suborbital tubercles, genal ridges absent; lower surface of head nearly glabrous; nearly impunctate; one pair of postlabial setae.

Paramedian groove represented by basal impression and short discal striole, latter extended approximately to middle of pronotum, and without pollinosity or punctures.

Basal scarp of elytron transverse, without prominence opposite base of Stria I; striae shallow, finely punctured; pollinosity limited to punctures; apical depression small, limited to apices of Striae I, II; apical tubercle not sinuate medially; metasternum with one median and two lateral longitudinal bands of punctures, otherwise impunctate; punctures of abdominal Sterna III-V in form of two irregular transverse rows (but less regular in arrangement than in *Plesioglymmius (sensu stricto)*); posterior row of each sternum as coarse as anterior row; female with lateral pits on Sternum IV and V, V slightly deeper; male with slight suggestion of these pits.

Male with ventral tooth on anterior femur, but without one on posterior femur; female without ventral tooth on either femur.

Only one species is known.

Plesioglymmius (Juxtaglymmius) jugatus new species
(Fig. 89,96,101)

Type material. – HOLOTYPE male, labelled: “JAVA” (MNHN). PARATYPE female, same data as type (MNHN).

Description. – Length 5.6–6.0 mm. As described for subgenus; head slightly wider than long; clypeus longer than wide, its sides parallel; eyes directed anterolaterally; temporal lobe rounded posteriorly and laterally; postorbital tubercle and posterior margin of temporal lobe pilose, notch between them glabrous (Fig. 96).

Pronotum relatively short, widest at middle, sides strongly curved to base and apex; disc of pronotum impunctate; marginal groove fine; prosternum, propleuron, and epipleura impunctate; pollinosity of prosternum limited to anterior margin and intercoxal pit.

Calcar of middle tibia small, acute; that of hind tibia broadly triangular, angle acute, well above level of tibial spur.

The tendency for the antennal bases to approach one another is seen throughout the genus. In this species it reaches its limit, with the antennal sclerites actually meeting in the midline. The bases of the antennae are separated by only slightly more than the width of one basal condyle so that it is difficult to see how they avoid interfering with one another.

This singular species has as much in common with *Ameroglymmius* of Brazil as it does with *Plesioglymmius (sensu stricto)* from nearby islands, and it may prove that the locality labels are erroneous.

Genus *Arrowina* Bell and Bell 1978
(Fig. 103-114)

Type species. – *Rhysodes taprobanae* Fairmaire 1873

Description. – Part I, 71.

Phylogeny. – With the exception of *A. taprobanae* and *A. pygmaea*, the members of this genus are all very different from one another. The most aberrant species is the Japanese *A. rostrata*, the only species which has an elongate rostrum and a femoral tooth. All the remaining species are confined to southern India and Ceylon. Although *A. anguliceps* and *A. nilgiriensis* are very different from one another, they share some common characters, such as a dilated orbital groove, that suggest that they are more closely related to one another than either is to *A. taprobanae* and *A. pygmaea*.

KEY TO SPECIES

1	Head almost twice as long as wide; anterior femur of male with ventral tooth (female unknown).....	<i>Arrowina rostrata</i> (Lewis), p.	439
1'	Head only slightly longer than wide; anterior femur of male without ventral tooth.....		2
2 (1)	Orbital groove absent; lateral margin of inner pronotal carina sloped gradually into paramedian groove		3
2'	Orbital groove complete, somewhat dilated; lateral margin of inner pronotal carina vertical, sharply defined		4
3 (2)	Metasternum with punctures confined to row along each margin; length 5.0 mm or more .		
	<i>Arrowina taprobanae</i> (Fairmaire), p.	439
3'	Metasternum with punctures in middle of disc as well as along margins; length 4.3 mm or less	<i>Arrowina pygmaea</i> new species, p.	441
4 (2')	Eyes large, deeper than long; posteromedial margin of temporal lobe sinuate posterior to medial angles.....	<i>Arrowina nilgiriensis</i> (Arrow), p.	441

- 4' Eyes reduced, longer than deep; posteromedial margin of temporal lobe not emarginate....
 *Arrowina anguliceps* (Arrow), p. 442

Arrowina rostrata (Lewis 1888)
 (Fig. 108,109)

Rhysodes rostratus Lewis 1888: 81.

Type material. – LECTOTYPE (here designated) male, labelled: “JAPAN: Oyayama, Higo District, G. Lewis, 1910-320 (Kyushu Island)” (BMNH). PARALECTOTYPE: According to the original description, there were two specimens, both males. The second specimen is not in the BMNH. If it is still extant, it is a paralectotype.

Description. – Length 5.5 mm. Antennal Segment XI short, almost spherical; stylet short, acuminate, larger than in other members of genus; head almost twice as long as wide, with rostrum distinctly elongate; postclypeal grooves sublinear; median lobe relatively broad, its posterior tip obtusely pointed, projected slightly above frontal pit; antennal groove fine, nearly linear; medial angles obtuse, distinctly separated; posteromedial margin emarginate between medial and occipital angles; orbital grooves obsolete; eye large, deeper than long; postorbital tubercle entirely absent (Fig. 109).

Pronotum narrow, elongate, length/greatest width about 1.40; widest anterior to middle; sides slightly curved, slightly convergent from widest point to base; markedly curved from widest point to apex; median groove of nearly even width, slightly expanded at posterior median pit, latter partly divided by constriction; paramedian grooves narrow, much narrower than inner carinae, and only slightly wider than median groove; lateral margin of inner carina vertical, sharply defined; marginal groove fine; prosternum and propleura impunctate.

Elytra elongate, lateral margins parallel in middle third; humeral tubercle well developed; elytral striae very shallowly impressed; stria punctures much finer than in other members of genus; elytral setae restricted to apex of Stria VII; metasternum impunctate; male with acute ventral tooth on anterior femur (female unknown); spurs of middle and hind tibiae nearly equal; calcar of hind tibia obtuse, raised slightly above level of tibial spurs.

The elongate rostrum, very narrow paramedian grooves, and absence of metasternal punctures are all diagnostic of this species.

Arrowina taprobanae (Fairmaire 1873)
 (Fig. 110-112)

Rhizodes taprobanae Fairmaire 1873: 389.

Type material. – HOLOTYPE female, labelled: “CEYLON” (MNH).

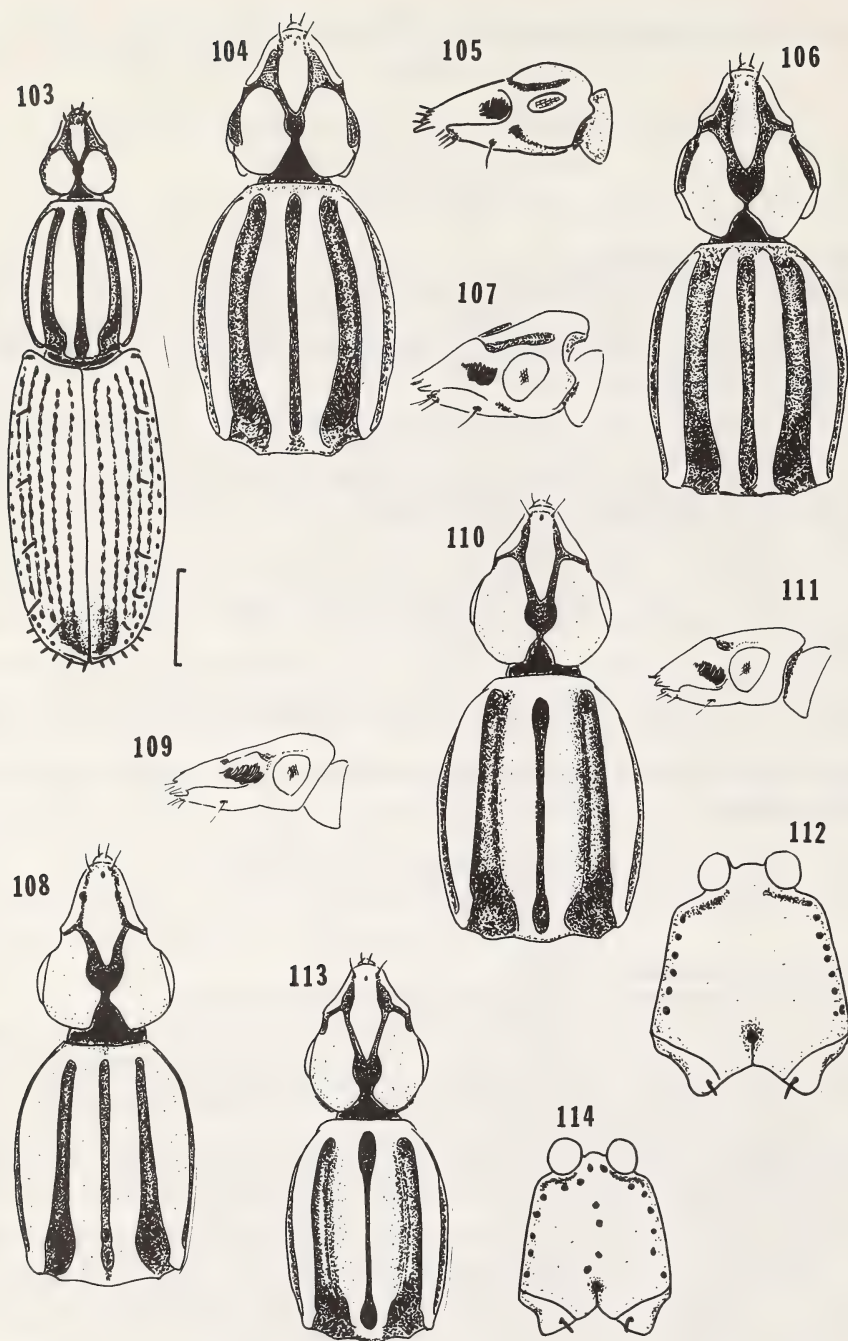
Description. – Length 5.0–6.2 mm. Antennal Segment XI slightly longer than wide; stylet very small but evident; head about 1.20 longer than wide; rostrum not elongate; postclypeal grooves dilated; median lobe otusely pointed posteriorly, its tip barely overhanging frontal pit; antennal groove narrow; medial angles nearly rectangular, almost contiguous, each angle slightly closer to occiput than to tip of median lobe; posteromedial margin very shallowly emarginate between medial and occipital angles; orbital groove absent; postorbital tubercle absent (Fig. 111).

Pronotum slightly longer than wide, length/greatest width 1.17; widest at middle, sides curved, apex markedly narrowed, base moderately so; inner carina wider than outer one; lateral margin of inner carina ill-defined, sloping gradually into paramedian groove; pronotum with one to two precoxal punctures on each side.

Elytra with lateral margins parallel in middle third; humeral tubercle well-developed, visible in dorsal view; elytral striae shallow, intervals nearly flat; stria punctures of inner striae moderate, those of outer striae coarse; basal puncture of Stria I enlarged; elytron with one seta in apex of Stria IV, one in apical striole, and several in apex of Stria VII; metasternum with row of coarse punctures along each margin, but without discal punctures (Fig. 112); female with deep lateral pits on abdominal Sternum V.

Middle and hind tibiae with spurs nearly equal, those of female much larger than those of male; ventral tooth absent from anterior femur; male with calcars well developed; hind calcar obtuse, distinctly raised above level of spurs.

This species and *A. pygmaea* differ from other members of the genus in having the lateral margin of the inner carina slope gradually into the paramedian groove. In all other species of *Arrowina*, the carina and the groove are separated by a sharply-defined, nearly vertical surface. Absence of discal punctures on the metasternum separates this species from *A. pygmaea*.



Figures 103 – 114. Genus *Arrowina*. Fig. 103-105, *A. anguliceps* (Arrow); Fig. 103, Habitus, dorsal aspect; Fig. 104, Head and pronotum, dorsal aspect; Fig. 105, Head, lateral aspect; Fig. 106,107, *A. nilgiriensis* (Arrow); Fig. 106, Head and pronotum, dorsal aspect; Fig. 107, Head, lateral aspect; Fig. 108,109, *A. rostrata* (Arrow); Fig. 108, Head and pronotum, dorsal aspect; Fig. 109, Head, lateral aspect; Fig. 110-112, *A. taprobanae* (Fairmaire); Fig. 110, Head and pronotum, dorsal aspect; Fig. 111, Head, lateral aspect; Fig. 112, Metasternum, metacoxae; Fig. 113,114, *A. pygmaea* new species; Fig. 113, Head and pronotum, dorsal aspect; Fig. 114, Metasternum, metacoxae.

Distribution. – Known with certainty only from Ceylon. Many specimens in MNHN, BMNH, AMS are labelled only with the name of the country. The only specimens we have seen with specific locality data are as follows: Three females, Dikoya, 3800-4200 feet; 6-XII-81 to 16-I-82, coll. G. Lewis (BMNH); one male, Maturata, no date, coll. Simon (MNHN); one female, Pundalaya, IV, 1888, coll. H.P. Green (BMNH). One male (probably from southern India rather than Ceylon), “Madura, Ind. Or.” from Loding, 1935 (MNHN). This almost certainly means the District of Madura (also spelled “Madurai”), and not the island of the same name near Java. The location is in the Tamil Nadu State, and is well to the east of the known ranges of other south Indian *Arrowina*. A specimen in MNHN, labelled: “Sydney, Austral”, surely has incorrect locality data. A record for Formosa by Miwa (1931), is probably a misidentification.

Arrowina pygmaea new species

(Fig. 113, 114)

Type material. – HOLOTYPE male, labelled: “CEYLON: Dikoya, coll. G. Lewis, 1910-320 (under label, 17-12-81)” (BMNH). Three PARATYPES one male, labelled: “CEYLON, Nuwara Eliya, 6234-8000 ft., 8-11-II-82, coll. G. Lewis 1910-320” (BMNH); one female, labelled: “CEYLON, coll. G. Lewis (no date), Sharp Colln. 1905-313” (BMNH); one male labelled: “CEYLON” (MNHN).

Description. – Length 4.0–4.4 mm. Very similar to *A. taprobanae*, with appearance of dwarf form of latter, but differing in following: head and pronotum relatively longer; elytra proportionally shorter; frontal grooves narrower, more linear; median lobe of head longer, its tip acute, clearly overhanging frontal pit; median angles of temporal lobes obtuse, distinctly separated; posterolateral end of antennal groove expanded, in form of rudimentary orbital groove; pronotum narrower and more elongate, slightly more narrowed at base; hind angle more nearly rectangular; elytral striae deeper, intervals slightly convex; elytral setae more numerous; three setae in Stria IV (one at base, one in middle, one at apex); one seta at apex of Stria VI; one on apical striole; several in apex of Stria VII; metasternum with coarse marginal punctures and several coarse punctures in middle of disc (in most specimens in form of median line (Fig. 114); in one specimen limited to group near anterior margin and few scattered on disc).

The coarse discal punctures on the metasternum and the much smaller size separate this species from *A. taprobanae*.

Arrowina nilgiriensis (Arrow 1942)

(Fig. 106, 107)

Rhysodes nilgiriensis Arrow 1942: 179.

Type material. – LECTOTYPE male, labelled: “INDIA: Nilgiri Hills, coll. Andrewes” (BMNH). Three PARALECTOTYPES two females (on same pin), same data as lectotype (BMNH); one female, same data as lectotype (MNHN).

Description. – Length 5.2–6.1 mm. Antennal Segment XI as wide as long; stylet minute, blunt, scarcely evident; head 1.25 times longer than wide; rostrum not elongate; postclypeal grooves widely dilated; median lobe obtusely pointed posteriorly, overhanging frontal pit; antennal groove dilated, short; frontal pit relatively broad; medial angles of temporal lobes nearly rectangular, contiguous; medial angles much closer to occipital angles than to tip of median lobe; posteromedial margin distinctly emarginate between medial and occipital margins; margin of temporal lobe oblique between eye and occipital angle, latter prominent; orbital groove dilated, extended to posterior margin of eye; eye large, deeper than long; postorbital tubercle large, deep, separated from temporal lobe by broad emargination in lateral view (Fig. 107).

Pronotum relatively short, length/greatest width is 1.12; widest at middle; sides curved; base moderately narrowed; apex markedly narrowed; paramedian grooves broad, almost as wide as inner or outer carinae; inner carina slightly wider than outer one at middle of pronotum; both margins of inner carinae sharply defined, separated from adjacent grooves by nearly vertical surfaces; about six precoxal punctures on each side of prosternum.

Elytra moderately elongate, sides nearly parallel in middle third; humeral tubercle well developed; elytral striae distinctly impressed; intervals convex; stria punctures coarse, those of inner striae elongate, those of outer striae rounded; basal puncture of Stria I not enlarged; Stria IV with four evenly spaced setae; one seta on medial surface of apical tubercle; about seven setae in apex of Stria VII; no setae in apical striole; metasternum with coarse marginal punctures, but without discal punctures; female with distinct lateral pits in abdominal Sterna IV and V, those of Sternum V deeper than those of Sternum IV; male with vestiges of lateral pits

in IV and V.

Male without ventral tooth on anterior femur; spurs of middle and hind tibiae strikingly unequal, anterior one of each pair less than 0.5 as long as posterior one; hind calcar very obtuse, raised high above spurs, its upper margin small notch about 0.33 of distance from spurs to base of tibia.

The prominent occipital angles of the head give this species much the appearance of *Omoglymmius* subgenus *Orthoglymmius*. It differs strikingly from the latter in the presence of two tibial spurs. The narrow pronotal carinae differentiate it from all *Orthoglymmius* except from *O. carinatus* (Grouvelle) and *O. hexagonus* Grouvelle. The latter two species differ from *A. nilgiriensis* in having conspicuously unequal elytral intervals.

Range. – Southern India, apparently confined to the Cardamum Mountains which form the boundary between Kerala and Tamil Nadu States. In addition to the type series, known from the following localities: one female, Chambagaganor, Madura (MMHN); one female, Cinchana, Anamalai Hills, 1050 m., IV-1957, coll. P.S. Nathan (BPBM), one female Shimbaganor (MNHN).

Arrowina anguliceps (Arrow 1901)
(Fig. 103-105)

Rhysodes anguliceps Arrow 1901: 89.

Type material. – LECTOTYPE (here designated) male, labelled: "S. INDIA, Pascoe Coll. 93-60" (BMNH). PARALECTOTYPES: one female, same data as male (BMNH). According to the original description, there are also two specimens in the Hope Department at Oxford. If these specimens still exist, they are also paralectotypes.

Description. – Length 5.8–6.9 mm. Antennal Segment XI longer than wide; stylet minute, scarcely evident; head 1.25 times longer than wide; rostrum not elongate; postclypeal grooves broadly dilated; median lobe short, its tip anterior to eye, its apex obtuse, not overhanging frontal pit; antennal groove dilated, short; frontal pit small and narrow; medial angles much closer to tip of median lobe than to occipital angles; medial angles obtuse, distinctly separated; posteromedial margin oblique between medial and occipital angles; margin of head rounded between eye and occipital angle; orbital groove dilated, extending beyond posterior margin of eye; its medial margin indistinctly defined; eye strongly reduced, lying entirely anterior to widest part of head, cornea flat, with only traces of facetting; eye longer than deep, with about 80 ommatidia; postorbital tubercle small, but more dorsal than in *A. nilgiriensis*, prominent in dorsal view (Fig. 105).

Pronotum rather elongate, length/greatest width is 1.29; widest point posterior to middle; sides markedly curved, base moderately narrowed, apex strongly narrowed; paramedian grooves broad, but somewhat narrower than outer carinae; both margins of inner carinae sharply defined, separated from adjacent grooves by nearly vertical surfaces; inner carina distinctly broader than outer carinae; marginal groove slightly dilated; about 12 precoxal punctures anterior to each coxal cavity and V-shaped line of punctures present on anterior part of prosternum.

Elytra short, oval, inflated; sides not parallel; humerus prominent, but humeral tubercle not visible in dorsal view; elytral striae slightly impressed; striae punctures very coarse, those of inner striae elongate oval, those of outer striae nearly round; punctures wider than intervals; latter convex; some punctures irregularly fused together, especially in humeral region, and near apical tubercle; basal puncture of Stria I not enlarged, but displaced laterally; Stria IV with up to four setae, when four are present they are evenly spaced, when setae are reduced, more anterior ones are missing; one seta on apical tubercle; none on apical striole; four to five in apex of Stria VII; hind wings reduced to small vestiges; metasternum with coarse marginal punctures, and with few discal ones anterior to coxae; female with shallow lateral pits in abdominal Sternum IV and deep ones in Sternum V; male with vestiges of pits in both Sterna IV and V.

Male without ventral tooth on anterior femur; all femora coarsely punctate on dorsal surface; spurs of middle and hind tibiae strikingly unequal, anterior one of each pair about 0.25 as long as posterior one; hind calcar of male obtusely rounded, its top distinctly proximad to tibiae, but not so proximad as in *A. nilgiriensis*. Penis illustrated in Part I, 68.

This is one of the most distinctive species in the tribe. The elytra are shorter and more convex than in other Rhysodini, suggesting those of *Dyschirius* (Scaritini). The reduced eye is unique within *Arrowina*, but is similar to that of *Tangaroa pensus*.

Range. – The Cardamum Mountains of southern India. The only definite locality record is a series of 12 specimens from Dodabetta Peak, 2475 m, III-11-62, coll. E.S. Ross, D.Q. Cavagnaro (CAS).

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¹This supplements the complete list of references found in Part I.

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REVISION AND CLADISTICS OF THE MIDDLE AMERICAN GENUS *CREAGROPHORUS* MATTHEWS (COLEOPTERA: LEIODIDAE)

QUENTIN D. WHEELER

Department of Entomology
The Ohio State University
Columbus, OHIO 43210
U.S.A.

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Creagrophorus is a compact genus of four Middle American species whose members eat fruiting bodies of puffballs (*Gasteromycetes*); *Creagrophorus hamatus* Matthews (Mexico, Panama), *Creagrophorus bihamatus* Matthews (Panama), *Creagrophorus jamaicensis* Peck (Jamaica), and *Creagrophorus spinaculeus* new species (Panama). A cladistic analysis led to the following conclusions: *Creagrophorus* is supported as a monophyletic group by apotypic broad labial palpus segment III with taeniaform seta, spines and flagellum of endophallus, absence of epicranial lines, and fimbriae of galeae and presence of four setae on segment I of the urogomphus of the larvae, transverse coxites and flattened, sclerotized styli of female genitalia, male femoral hooks (denticles), expanded middle tibia, and puffball ecological relationships; the *Aglyptinus* association is a monophyletic lineage consisting of *Creagrophorus*, *Aglyptinus*, and *Scotocryptini*, and defined synapotypically by 3-3-3 tarsi and oblique lines on abdominal sternum III; *Aglyptinus* is the sister group of *Creagrophorus-Scotocryptini*; *Scotocryptini* is the sister group of *Creagrophorus*; *C. hamatus* is the sister to the *jamaicensis-bihamatus-spinaculeus* lineage, and *C. bihamatus* sister species to *C. spinaculeus*. *Creagrophorus* is hypothesized to be an endemic Middle American genus, which arose after its ancestor migrated from South America where the sister group differentiated in body structure and ecological relationships (*Scotocryptini*); the *hamatus* lineage was isolated north of the Isthmus of Tehuantepec; the *jamaicensis* lineage was isolated in nuclear Middle America (and dispersed to Jamaica); and *bihamatus/spinaculeus* became north/south vicariants due to volcanism in the Chiriqui region. *Creagrophorus* beetles are continental in differentiation pattern, and as such are implied to have wide geographic ranges and require relatively long periods of time for speciation. The *Aglyptinus* association and *Creagrophorus* are defined, species of *Creagrophorus* described, and the following presented; keys to genera of *Aglyptinus* association and species of *Creagrophorus*, habitus drawings of adult and larval beetles, illustrations of important character states and geographic distribution, designation of lectotypes for Matthews' species, and discussions about ecological, cladistic, and zoogeographic relationships.

Creagrophorus est un petit genre de Leiodidae d'Amérique Centrale comprenant quatre espèces qui se nourrissent de vesses-de-loup (champignons *Gastéromycètes*); ce sont: *C. hamatus* Matthews (Mexique et Panama), *C. bihamatus* Matthews (Panama), *C. jamaicensis* Peck (Jamaïque) et *C. spinaculeus* Wheeler, une espèce nouvelle (Panama). Une analyse cladistique permet de tirer les conclusions suivantes; les *Creagrophorus* forment un taxon monophylétique, à cause de la présence des caractères apotypiques suivants: troisième segment des palpes labiaux large et portant une soie taéniaforme, phallobase avec épines et flagelle, absence de lignes épicaniales et de fimbriae sur les galéas, présence de quatre soies sur le premier segment de l'urogompe chez les larves, coxas transversaux et aplatis, stylets de l'armature génitale des femelles sclérifiés, fémurs des mâles portant des crochets (denticules), tibias intermédiaires élargis, et rapports écologiques avec les vesses-de-loup; le groupe *Aglyptinus* constitue une lignée monophylétique et comprend les *Creagrophorus*, les *Aglyptinus* et les *Scotocryptini*. Ce groupe est défini par les synapomorphies suivantes: formule tarsale 3-3-3, et présence de lignes obliques sur le troisième sternite abdominal. Le genre *Aglyptinus* est monophylétique et est apparenté aux *Creagrophorus-Scotocryptini*. *C. hamatus* est apparenté à la lignée *jamaicensis-bihamatus-spinaculeus* et *C. jamaicensis* est apparenté à la lignée *bihamatus-spinaculeus*. On pose comme hypothèse que *Creagrophorus* est un genre endémique à l'Amérique Centrale et qu'il est apparu à la suite de la migration vers le nord de son ancêtre de l'Amérique du Sud, où le groupe apparenté (*Scotocryptini*) s'est différencié morphologiquement et écologiquement. La lignée *hamatus* a été isolée au nord de l'isthme de Tehuantepec tandis que la lignée *jamaicensis* a été isolée au cœur de l'Amérique Centrale (et s'est dispersée jusqu'en Jamaïque). Finalement, *C. bihamatus* et *C. spinaculeus* sont devenus des vicariants, le premier au nord, le second au sud, en raison de l'activité volcanique dans la région de Chiriqui. Étant donné que les *Creagrophorus* ont un patron de différenciation continental, ils devraient avoir une distribution couvrant de vastes régions géographiques et leur processus de spéciation devrait s'étendre sur une période de temps relativement longue. On définit le groupe *Aglyptinus* et les *Creagrophorus*, et on

décrit les espèces de *Creagrophorus*. On présente aussi une clef d'identification pour chacun des genres faisant partie du groupe *Aglyptinus* et pour les espèces de *Creagrophorus*, ainsi que des illustrations de l'aspect général des larves et des adultes, des illustrations des principaux caractères et des cartes montrant la distribution géographique. On désigne des lectotypes pour les espèces décrites par Matthews, et enfin on discute des rapports écologiques, cladistiques et biogéographiques.

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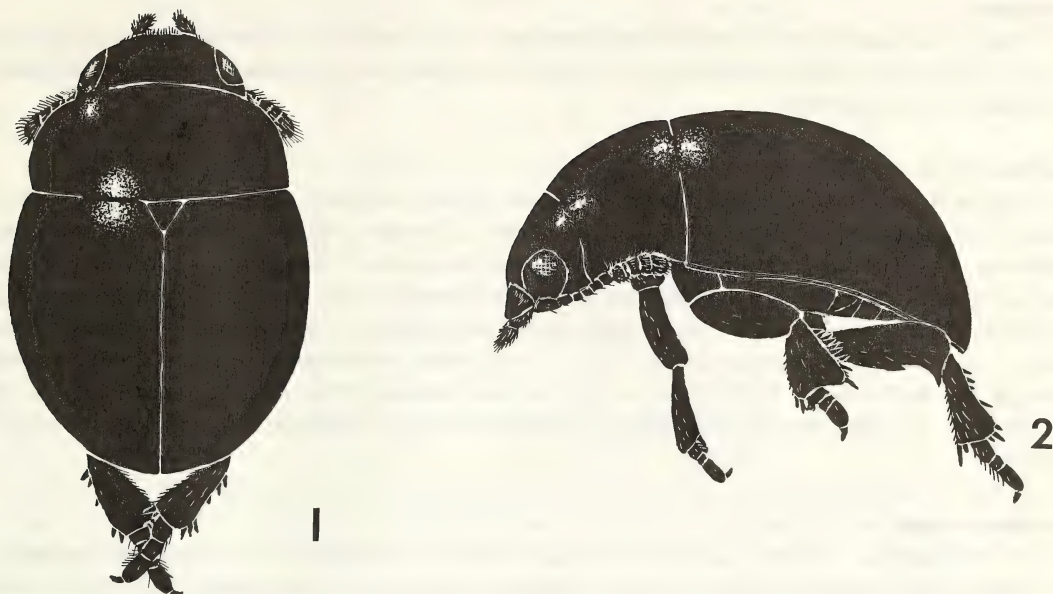
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INTRODUCTION

Small, convex, shiny beetles (Fig. 1,2) which comprise the leiodid genus *Creagrophorus* Matthews are distributed in Middle America, from central Mexico south to Panama, and in Jamaica in the Antilles (Peck, 1972). Their minute size and obscure ecological habits have made these beetles exceedingly rare in museum collections. During recent field investigations on tropical, lowland, terrestrial carabids for Terry L. Erwin (National Museum of Natural History) in Panama, I collected a large series of adults and larvae of an undescribed species and, perhaps more significantly, information about the ecological relationships of *Creagrophorus*.

Taxonomy of *Creagrophorus* has remained largely neglected since the generic description by Matthews in 1888. Peck (1977a) pointed out inconsistencies between the tarsal formula of his Jamaican species and the formula recorded by Matthews for his species. Following Peck's suggestion, I have re-examined Matthews' types and found that they, as well as Peck's species, have 3-3-3 tarsi.

Creagrophorus, together with *Aglyptinus* and the Scotocryptini apparently form a monophyletic group which I define below as the taxonomically informal *Aglyptinus* association of genera. Members of this lineage were used as the out-group for determination of character polarity in *Creagrophorus*. Lack of specimens has made decisions about cladistic and zoogeographic relationships difficult. However, sister group relationships are hypothesized using existing information about structure and ecology of *Creagrophorus* and related genera, and a few cursory observations are made about *Creagrophorus* zoogeography, based on the cladistic conclusions.



Figures 1 – 2. *Creagrophorus spinaculeus*, habitus: Fig. 1, dorsal aspect; Fig. 2, lateral aspect.

The purposes of this study are to define the genus *Creagrophorus*, revise known species, discuss ecological, cladistic (intrageneric and suprageneric), and zoogeographic relationships, and describe the larvae of a member of *Creagrophorus*.

MATERIALS AND METHODS

Materials

This study is based on about 65 adult and larval *Creagrophorus*, including type-specimens for three previously described species. Specimens of the following species were studied as out-group taxa, and voucher specimens placed in the National Museum of Natural History (USNM, listed below): *Scotocryptus* sp., *Aglyptinus laevis* (LeConte), *Aglyptinus matthewsi* Champion, *Aglyptinus* sp. (Panama), and a new species of *Aglyptinus* to be described elsewhere. The following acronyms represent collections from which material was borrowed, or into which type material is deposited:

- BMNH British Museum (Natural History), London;
- CNCI Canadian National Collection of Insects, Ottawa;
- MCZC Museum of Comparative Zoology, Cambridge;
- OSUC Ohio State University, Columbus;
- QDWC Author's private collection, Columbus;
- USNM National Museum of Natural History, Washington.

Methods

I have generally followed those methods discussed in a previous leiodid study (Wheeler, 1979), including both philosophical and procedural methods. Exceptions, modifications, and additions to those methods are discussed below.

Species criteria

I use both the theoretical and practical criteria for defining and recognizing species here as in my study of *Anisotoma* (Wheeler, 1979). Because so few specimens of *Creagrophorus* were available, delimitation of the range of intraspecific variation was impossible. I have used the structure of the aedeagus, particularly the endophallus, as a source of structures on which decisions regarding separation of species were made. Eversion of the endophallus was only possible in one species *C. spinaculeus*, since so few males were seen. Consequently, drawings of endophallus structures were prepared by observation through the median lobe. While these are only approximations of the actual detailed structure of endophallus armature, they do show distinct differences in size, number, and configuration of spines present.

Cladistic methods

My philosophical approach is essentially that of Hennig (1965,1966), as discussed previously (Wheeler, 1979). Criteria for determination of character polarity were discussed in detail by Munroe (1974) and Ekis (1977), and cladistics generally outlined by Griffiths (1972), and need not be pursued here. I have based my decisions about character polarity on out-group comparisons with taxa of the *Aglyptinus* association of genera.

Classification methods and formal ranking

My classifications of species and genera are phyletic sequence classifications as formulated and applied by Nelson (1972, 1973), Cracraft (1974), Schuh (1976), and Wheeler (1979). No formal rank is assigned to the monophyletic lineage formed by *Creagrophorus* and related genera. Rather, the informal *Aglyptinus* association of genera is proposed and defined. This allows present statements about cladistic relationships, and avoids premature reranking of Leiodini taxa before global studies are made, as suggested by Erwin (1975) as a general taxonomic rule. Similarly, I refrain from reranking the Scotocryptini now, but do state my views as to their phylogenetic significance.

Examination of larvae

Larvae were collected and stored in 70% ethanol until studied. For examination, they were cleared in Nesbitt's solution at room temperature and mounted directly into Hoyer's medium (Krantz, 1978). Magnifications up to X450 were used for observation and drawing.

Disarticulation

In addition to use of standardized dissecting methods for male and female genitalia (Wheeler, 1979), it is important to make disarticulations of entire beetles whenever possible. Inaccurate interpretations of detailed structure (e.g. tarsomere numbers in *Creagrophorus* and *Aglyptinus*, etc.) have plagued leiodid classification, but can be avoided by use of high magnification with disarticulated specimens as comparison of structures is enhanced and many additional characters are available for cladistic analysis. After disarticulation of relaxed and partially cleared specimens, parts are further cleared in dilute KOH, rinsed in water, and stored and studied in a mixture of glycerin and glycerin jelly as applied elsewhere by Wheeler (1979) and Triplehorn and Wheeler (1979). Thus parts may be oriented for view from any

angle with the use of gentle heat, yet are held firmly enough for preparation of accurate drawings. I subscribe to the views of Watrous (In press), who discusses both practical and philosophical reasons for preparing disarticulations in relation to his work with *Lathrobium* staphylinid beetles.

Descriptive format

All of the species could not be studied in the same detail as *C. spinaculeus*. Therefore, *C. spinaculeus* is described in considerable detail (including larvae), the genus diagnosed and presumed to share characters of that species except as noted, and other species diagnosed and briefly described. Where appropriate, the following are given for each species: type data, diagnostic combination, description, geographic relationships, cladistic relationships, material examined, and illustrations. Measurements were made as discussed previously (Wheeler, 1979), and are only approximations due to varying contractability of individual specimens.

COMMENTS ON FUNCTIONAL MORPHOLOGY

Aside from my observations of adult and larval *C. spinaculeus* in Panama, nothing is known about *Creagrophorus* habits. During the present study, I have developed ideas about possible functions of some structures of adult beetles. I present these ideas as possible explanations for the structures. Certainly other explanations are not difficult to conceive, but at least my ideas may stimulate further field observations which can test them and suggest realistic alternatives.

Female genitalia (Fig. 33)

Flattened, sclerotized styli of the female genitalia contrast so sharply with the plesiotypic form (i.e., lightly sclerotized, digitiform) seen in the sister group and Leiodinae in general that some specialized function is strongly implied. I hypothesize that it is an adaptation for piercing the hardened outer wall of host puffball fruiting bodies making oviposition possible, or perhaps for cutting through tough outer walls of immature fruiting bodies before their emergence above ground (see discussion under "Legs" below). Oviposition preceding apical pore formation by the host is supported by my observations in the field, although there is no reason why older fruiting bodies could not be used at times, beetles gaining entry through the apical pore.

Legs. (Fig. 16-19, 21, 22-26)

Enlargement of tibiae, presence of spines, and compaction of tarsomeres all may indicate fossorial habits. Most puffballs develop under ground until maturity, and it is conceivable that *Creagrophorus* beetles seek them out. "Primitive" Leiodini (e.g., *Leiodes* spp.) feed on hypogeous fungi (e.g., truffles: see Arzone 1970, 1971), and *Creagrophorus*, like other leiodines, retain the antennal vesicles (Crowson, 1967; Peck, 1977b), which are presumably chemoreceptive. Subterranean activities aside, adult beetles must move within the fruiting bodies in order to emerge, and these consist internally of little more than a large mass of spores. Male femoral hooks are another matter (Fig. 11-14). I do not believe they function directly in copulatory activities (males have spatulate adhesive setae on tarsomeres), but rather in some male/male aggression or male/female courtship behavior.

Mouthparts

Distinct molar teeth are not present on adult (Fig. 8,9,28) or larval (Fig. 6,64) mandibles. Such teeth were proposed as spore-crushing devices in *Anisotoma* beetles which feed on slime mold spores (Wheeler, 1979). Crenulations (Fig. 9) of adult mandibles may be homologous with these teeth, and the

molar region probably still functions in spore crushing to some extent. Setae and spines of the maxillae in adults and larvae (Fig. 29,62) probably help to rake spores into the mouth. The strangest modification of the mouthparts is the taeniaform seta of the labial palpus (Fig. 3,30), for which I do not hazard a functional explanation.

The *Aglyptinus* association of genera

Creagrophorus, *Aglyptinus*, and Scotocryptini appear to consitute a monophyletic lineage. Synapotypic character states which support this arrangement are discussed more fully under "Cladistics", but include the 3-3-3 tarsomere configuration and oblique lines of the first visible abdominal sternum (sternum III). I have not made a study of Scotocryptini genera(*Scotocryptus*, *Parabystus*, *Synaristus*, and *Scotocryptodes*), and I am therefore not in a position to resolve specific problems in that taxonomic group. The current classification is based on what I perceive as weak taxonomic characters (Portevin, 1907,1937; Hatch, 1929a), and all members of Scotocryptini need to be re-examined in detail. For the purposes of this study of *Creagrophorus*, I have made the following assumptions about Scotocryptini: first, that Scotocryptini is a monophyletic group, and second, that the single species of *Scotocryptus* which I have studied is representative of this monophyletic lineage. An inevitable conclusion, if the above taxonomic arrangement is correct, is that Scotocryptini should not be allotted tribal rank. Until a study of these beetles can be made, however, I conservatively refrain from re-ranking the Scotocryptini. Nonetheless, I am convinced that it is a phylogenetically indefensible taxonomic rank.

Table 1. Phyletic sequence classification of *Aglyptinus* association genera and *Creagrophorus* species, and geographic distributions of taxa in North America (NAM), nuclear Middle America (nMA), the Antilles (ANT), southern Middle America (sMA), and South America (SAM). Numbers beside supraspecific taxa indicate number of species in area.

Taxon	NAM	nMA	ANT	sMA	SAM	Sister Group
<i>Aglyptinus</i> Cockerell	1	3	5	2	9	Middle and South America
Scotocryptini (4 genera)	2	0	0	1	6	Middle America
<i>Creagrophorus</i> Matthews	1	0	1	3	0	South and Middle America
<i>C. hamatus</i> Matthews	+	—	—	+	—	nMA and sMA
<i>C. jamaicensis</i> Peck	—	—	+	—	—	sMA
<i>C. bihamatus</i> Matthews	—	—	—	+	—	sMA
<i>C. spinaculeus</i> Wheeler	—	—	—	+	—	sMA

KEY TO GENERA OF THE *AGLYPTINUS* ASSOCIATION

Adults

- 1 Tarsi 3-3-3; abdominal sternum III with oblique lines (Fig. 34), *Aglyptinus* associaton.. 2
- Tarsal formula greater than 3-3-3; sternum III without oblique lines (other Leiodini genera, not in key)
- 2 Antennal club compact; tarsi compact, tarsomeres subcylindrical 3
- Antennal club loosely articulated; tarsi very long, thin; usually associated with fungi *Aglyptinus* Cockerell
- 3 Eyes present; body glabrous; labial palpus with taeniaform seta (Fig. 30); stylus of female genitalia flattened, heavily sclerotized (Fig. 33); middle tibia wider than hind tibia..... *Creagrophorus* Matthews
- Eyes absent; body pubescent; labial palpus without taeniaform seta; stylus long, digitiform; middle tibia not wider than hind tibia Scotocryptini (Includes following genera: *Scotocryptus* Girard, type species *Scotocryptus meliponae* Girard; *Parabystus* Portevin, type species *Scotocryptus inquilinus* Matthews; *Synaristus* Portevin, type species *Synaristus pilosus* Portevin; and *Scotocryptodes* Portevin, type species *Scotocryptodes germaini* Portevin. Key in Hatch, 1929a).

Genus *Creagrophorus* Matthews

Type species. – *Creagrophorus hamatus* Matthews, 1888, by subsequent designation (Hatch, 1929b).

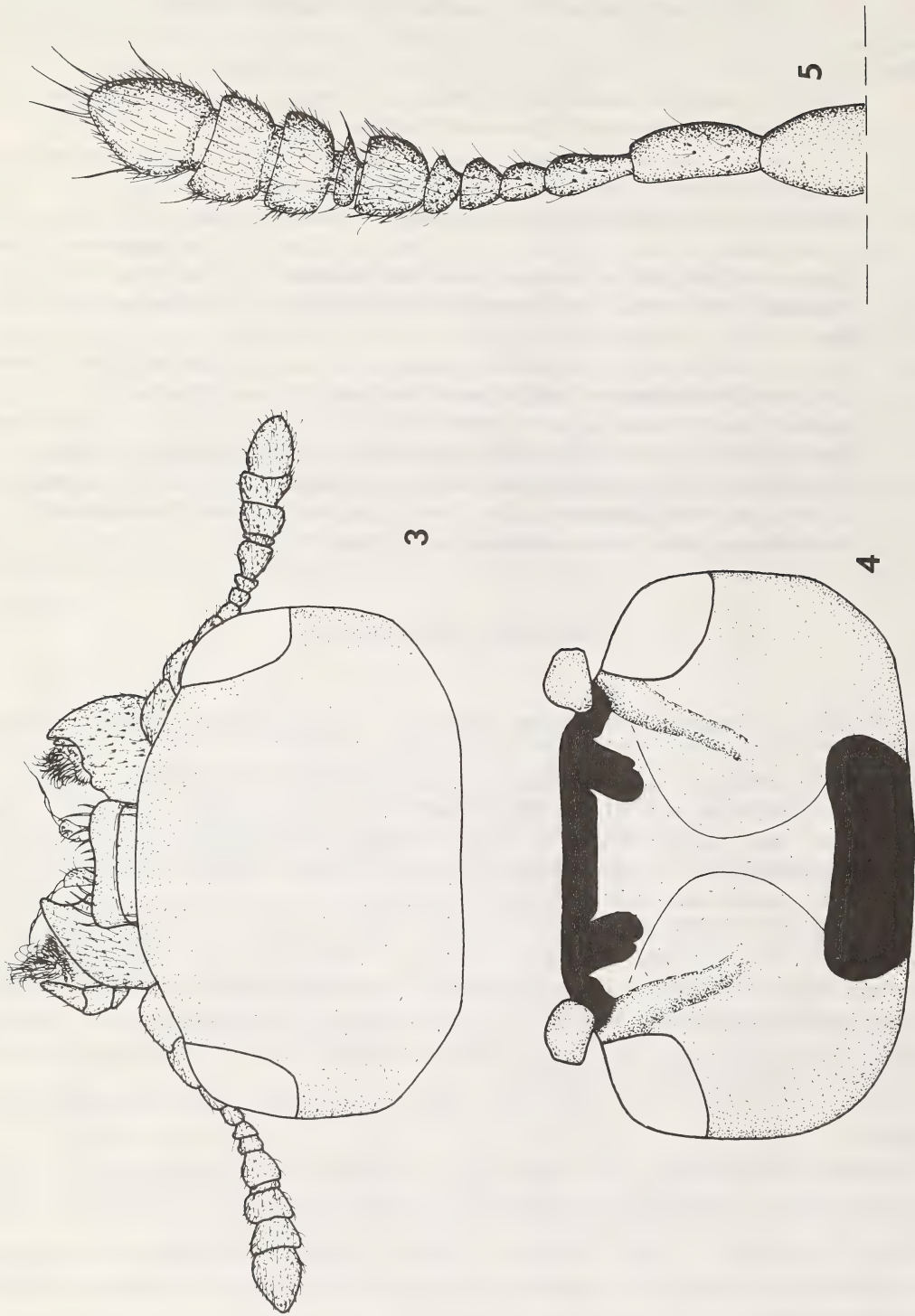
Diagnostic combination. – Staphylinoidae; Leiodidae; Leiodinae; Leiodini; ADULTS (Fig. 1,2) – Tarsi 3-3-3; abdominal sternum III with oblique lines (Fig. 34); spermathecal capsule short, broad, cylindrical, with long distal process (Fig. 35); stylus of female genitalia flattened, markedly sclerotized (Fig. 33); aedeagus ventrally curved, endophallus with large annulate flagellum and various spination (Fig. 36-40,50); middle tibia wider than hind tibia; antennal club of five antennomeres, compact (Fig. 5), antennomere VIII smaller than VII or IX; tarsi compact, subcylindrical (Fig. 24); labial palpus with taeniaform seta apically (Fig. 30); LARVAE (Fig. 53) – Galea not fimbriate (Fig. 62); epicranial lines absent (Fig. 54); urogomphal article I quadrisetose, one seta very long (Fig. 58), segment II long, crenulate; terga of abdomen each with four forked dorsal setae and one pointed lateral pair (Fig. 55); sterna with simple setae only (Fig. 56); ECOLOGICAL RELATIONSHIPS – Adults and larvae feed on fruiting bodies of puffballs (Gasteromycetes).

Cladistic relationships. – The sister group appears to be Scotocryptini, as discussed under ‘Cladistics’.

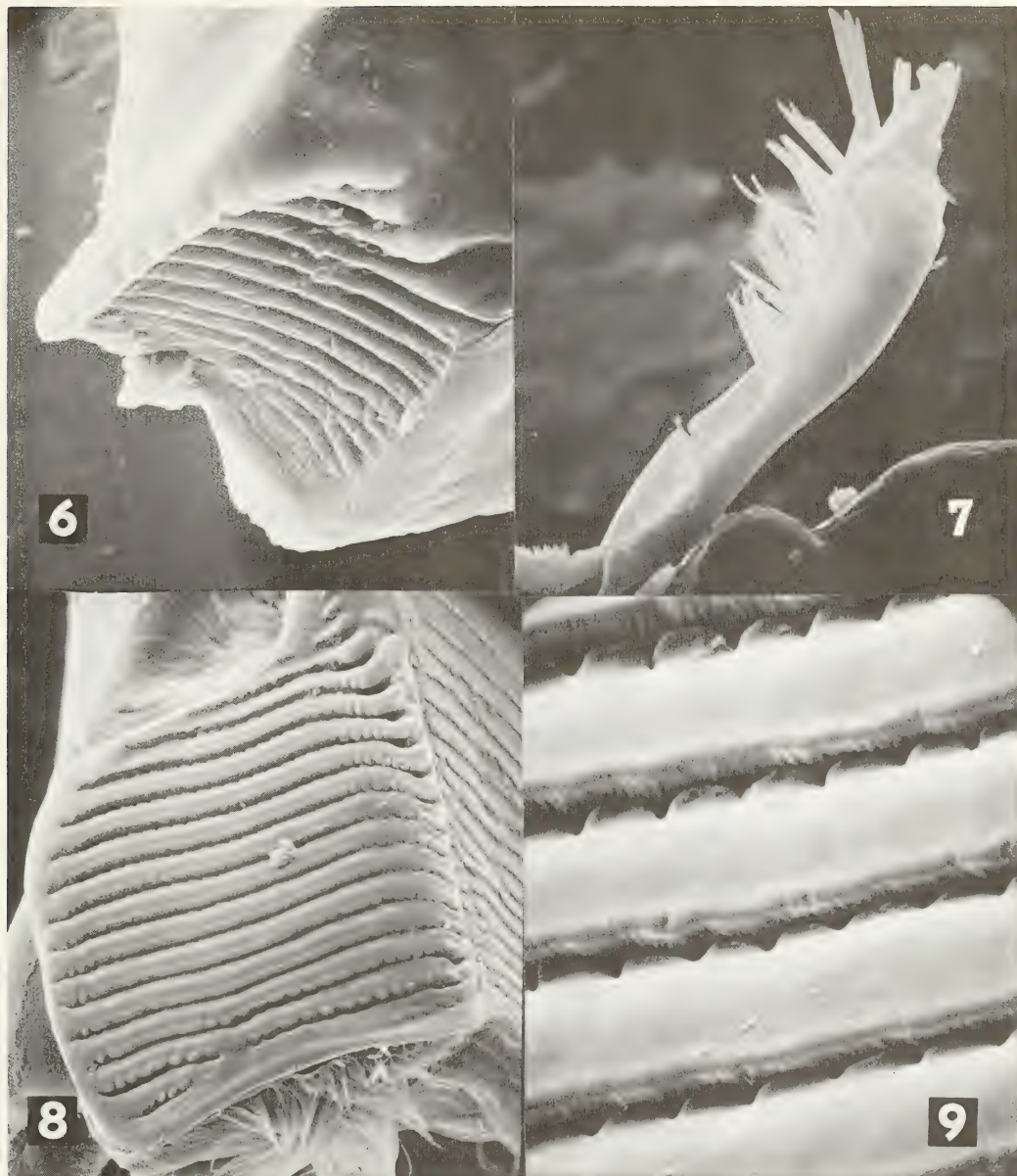
Geographic relationships. – The sister group is primarily South American with a northern subtraction pattern; *Creagrophorus* is entirely Middle American including political divisions Mexico, Panama, and Jamaica. Relationships discussed in detail under ‘Zoogeography’ section.

Species classification. – Table 1 represents a phyletic sequence classification of the species of *Creagrophorus*, and members of the *Aglyptinus* association. It is based on relationships concluded from the cladistic analysis.

Semaphoronts. – Key and descriptions of adult beetles are followed by a discussion and description of larvae.



Figures 3 – 5. *C. spinaculeus*: Fig. 3, head, dorsal aspect; Fig. 4, head, ventral aspect; Fig. 5, antenna.



Figures 6 – 9. *C. spinaculeus*: Fig. 6, mola, larval mandible; Fig. 7, prostheca, adult mandible; 8-9, mola, adult mandible.

KEY TO ADULT *CREAGROPHORUS*

- 1 Elytral punctures distinct; hind femur with single hook (Fig. 12); middle femur with hook (Fig. 11); endophallus with small spines near middle (Fig. 36); Mexico, Panama..... *Creagrophorus hamatus* Matthews, p. 458
- Elytral punctures indistinct or absent; hind femur with two hooks (Fig. 14); middle femur without hook (Fig. 10); endophallus with more extensive spination; Panama or Jamaica ... 2
- 2 Color black; endophallus with patches of very large spines near apex (Fig. 39,40); median lobe dorsally curved near apex (Fig. 41); Panama *Creagrophorus spinaculeus* new species, p. 456
- Color reddish-brown; endophallus with patches of smaller spines (Fig. 38) or small spines only (Fig. 37), lacking patches of large spines..... 3
- 3 Endophallus with small spines only (Fig. 37), lacking patches of large spines; female middle tibia about as wide as in male; Jamaica *Creagrophorus jamaicensis* Peck, p. 461
- Endophallus with two longitudinal patches of larger spines (Fig. 38); female middle tibia much narrower than in male; Panama *Creagrophorus bihamatus* Matthews, p. 458

Creagrophorus spinaculeus new species
(Fig. 1-10,13,15-19,22,23,27-35,39-43,69)

Holotype. – Male, USNM.

Type locality. – PANAMA, Canal Zone, Barro Colorado Island.

Paratypes. – 20, same locality as holotype; BMNH (2 males, 2 females), CNCI (2 males, 2 females), MCZC (1 male, 2 females), USNM (1 male, 7 females), QDWC (1 male).

Diagnostic combination. – Color black; shining; male hind femur bidentate (Fig. 13); female middle tibia similar to that of male; endophallus with patches of large spines near apex (Fig. 39,40).

Description. – Form subhemispherical (Fig. 1,2); length about 1 mm.

Color. Black, mouthparts, legs, and venter paler.

Microsculpture. Micropunctules distinct, moderately dense on head, increasingly sparse and obscure on pronotum and elytra.

Luster. Shining.

Head. Obovate, transverse (Fig. 3). Eyes large, conspicuous not protruding (Fig. 3). Postocular tempora not developed. Antennal grooves ventral (Fig. 4). Gular sutures subparallel at middle, divergent anteriorly and posteriorly. Antennae short, club compact, antennomeres as illustrated (Fig. 5).

Mouthparts. Labrum (Fig. 31) with six pairs apical setae, setae I-V increasing in length, VI shorter. Mandibles (Fig. 28) short, robust; apical dens large, pointed, grooved on inner margin; prostheca large, with mesal, forked cuticular processes (Fig. 7); mola with transverse grooves lined with crenulations (Fig. 8,9). Maxilla: three palpomeres, palpomere III aciculate (Fig. 29); lacinia and galea with dense tufts of fine setae. Labium: three palpomeres, III broad, curved, with several long setae medially and broad taeniaform seta apically (Fig. 30), taeniaform seta about length of palpus.

Thorax. Pronotum wider than long (Fig. 1); anterior margin medially excised; disc broadly curved. Prosternum short, medially carinate, carina forming ventrally-directed, bidentate, laminiiform process. Procoxal cavities closed anteriorly and posteriorly. Mesosternum carinate; posterior intercoxal process declivous, forming transverse laminiiform process. Hind wings long. Elytra broad, sutural stria complete, epipleural fold very wide basally, gradually narrowed posteriorly (Fig. 27).

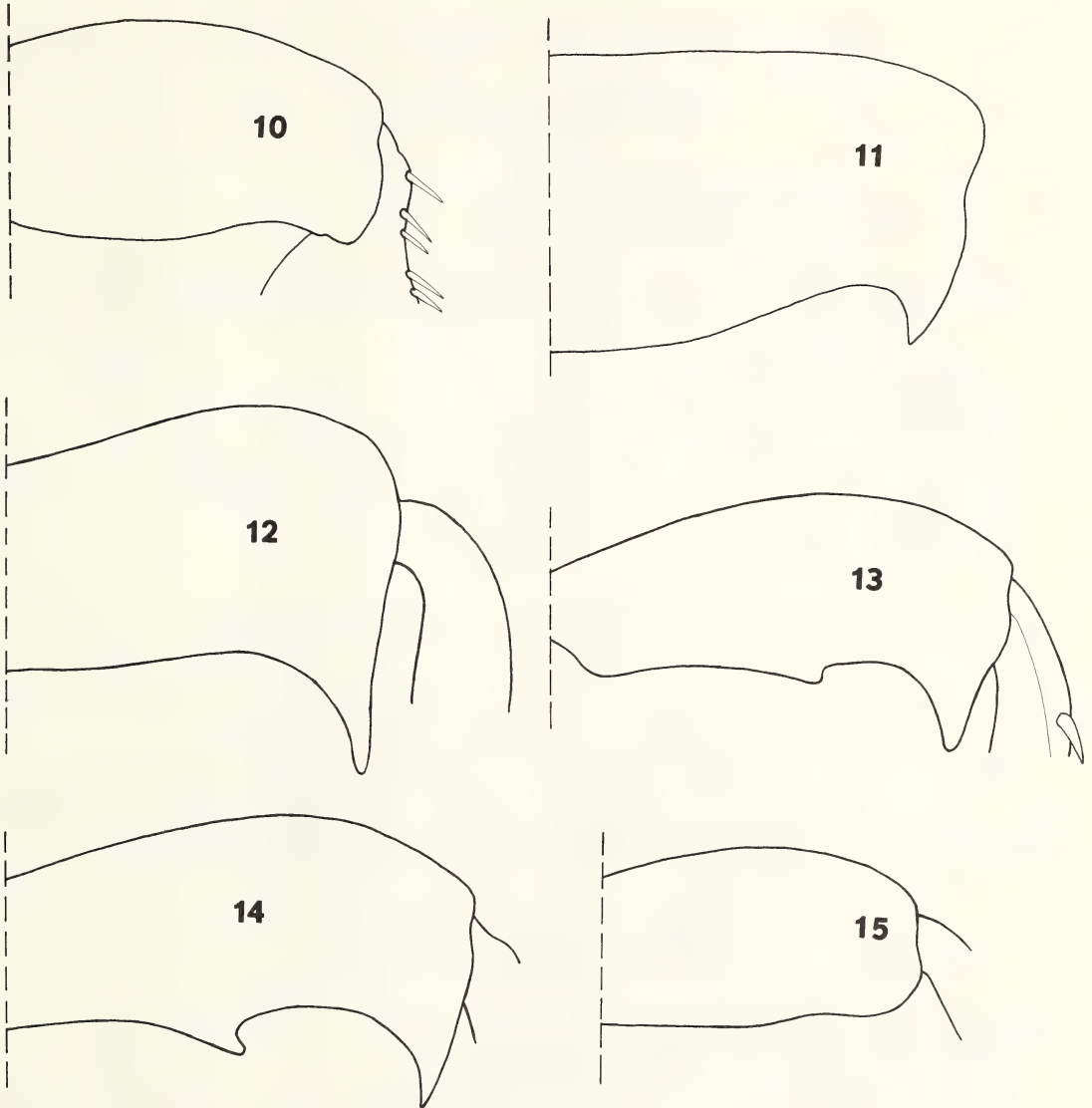
Legs. Tarsal formula 3-3-3, tarsomeres compact, subcylindrical (Fig. 17); basal tarsomere of male front and middle legs with spatulate setae (Fig. 16,18). Front tibia narrow (Fig. 16). Middle tibia greatly enlarged (Fig. 17,18,19), much wider than hind tibia (Fig. 22,23), with many stout spines. Hind tibia gradually widened. Middle femur wide. Hind femur wide (Fig. 13,15), bidentate in male (Fig. 13).

Abdomen. Sterna III-VIII visible, III-VII each with a single, transverse row of fine setae, VIII with medial and apical rows. Sternum III with oblique lines (Fig. 34).

Male genitalia. Median lobe widest subapically, narrowed at apex (Fig. 42); generally curved ventrally, apex curved dorsally (Fig. 41). Endophallus with large annulated flagellum, and apical patches of large setae (Fig. 39,40). Parameres as illustrated (Fig. 43).

Female genitalia. Coxites broad, transversely oriented. Styli laterally curved, flattened, sclerotized, each with single stout seta and finer mesal setae (Fig. 33).

Spermatheca. Capsule short, broad, cylindrical, with tubular distal process, short tubular basal process, long, tubular, sclerotized duct leading to longer membranous duct (Fig. 35). Spermathecal gland small, membranous, inserted basally at side (Fig. 35).



Figures 10 – 15. *Creagrophorus* spp., femora: Fig. 10, *C. spinaculeus*, male, middle leg; 11, *C. hamatus*, male, middle leg; Fig. 12, *C. hamatus*, male, hind leg; Fig. 13, *C. spinaculeus*, male, hind leg; Fig. 14, *C. bihamatus*, male, hind leg; Fig. 15, *C. spinaculeus*, female, hind leg.

Geographic relationships. – This species is known only from the Canal Zone in Panama. Both *C. hamatus* and *C. bihamatus* seem to occur in Chiriqui Province, Panama. Full ranges of all three species are undetermined.

Cladistic relationships. – *C. spinaculeus* is the sister species of *C. bihamatus*, based on synapotypic occurrence of patches of large spines on the endophallus (Fig. 38,39,40).

Material examined. – In addition to specimens designated as types, one male and one female were disarticulated and are in my collection (QDWC). Illustrations were made primarily from these specimens.

Larvae. – The larvae are described under a section following descriptions of adults.

Creagrophorus hamatus Matthews
(Fig. 11,12,20,25,26,36,50-52,69)

Creagrophorus hamatus Matthews, 1888: 83.

Lectotype. – Male, BMNH, here designated (examined).

Type locality. – MEXICO, Puebla.

Diagnosis combination. – Elytral punctation distinct; male middle femur with hook (Fig. 11), hind femur with single hook (Fig. 12); reddish-brown in color; area of endophallus near middle with small spines (Fig. 36).

Description. – Length about 2.3 mm.

Color. Reddish-brown, appendages more yellowish.

Microsculpture. Sparse, fine punctules on head and pronotum, slightly larger, irregularly distributed punctules on elytra.

Luster. Shining.

Legs. Male middle tibia clavate apically (Fig. 26); middle femur with single hook (Fig. 11); hind tibia slightly clavate (Fig. 25); hind femur with single hook (Fig. 12).

Male genitalia. Median lobe ventrally curved (Fig. 50); narrowed apically (Fig. 51). Paramere fused to median lobe, in part (Fig. 52). Endophallus with small spines confined to area near middle (Fig. 36).

Female. – I have seen no females of this species.

Geographic relationships. – This is the only species of *Creagrophorus* known to occur as far north as Mexico. Matthews (1888) also records the species from Chiriqui where *C. bihamatus* also occurs.

Cladistic relationships. – *C. hamatus* is the sister of remaining species, the *jamaicensis-bihamatus-spinaculeus* lineage. The latter species share synapotypic character states including bidentulate male hind femora, and more extensive spination of the endophallus.

Material examined. – The lectotype specimen only, labelled: SYN-TYPE (circular, ringed with blue)/TYPE (circular, ringed with red)/Puebla (hand-written), Mexico. Salle coll./hamatus (hand-written)/B.C.A., Col.,II,I./*Creagrophorus hamatus* Matt. ♂ (hand written) det Hlisenkovsky 1961/*Creagrophorus hamatus* Matth., M.E.Bacchus det 197, SYNTYPE/and my labels.

Creagrophorus bihamatus Matthews
(Fig. 14,21,24,38,47-49,69)

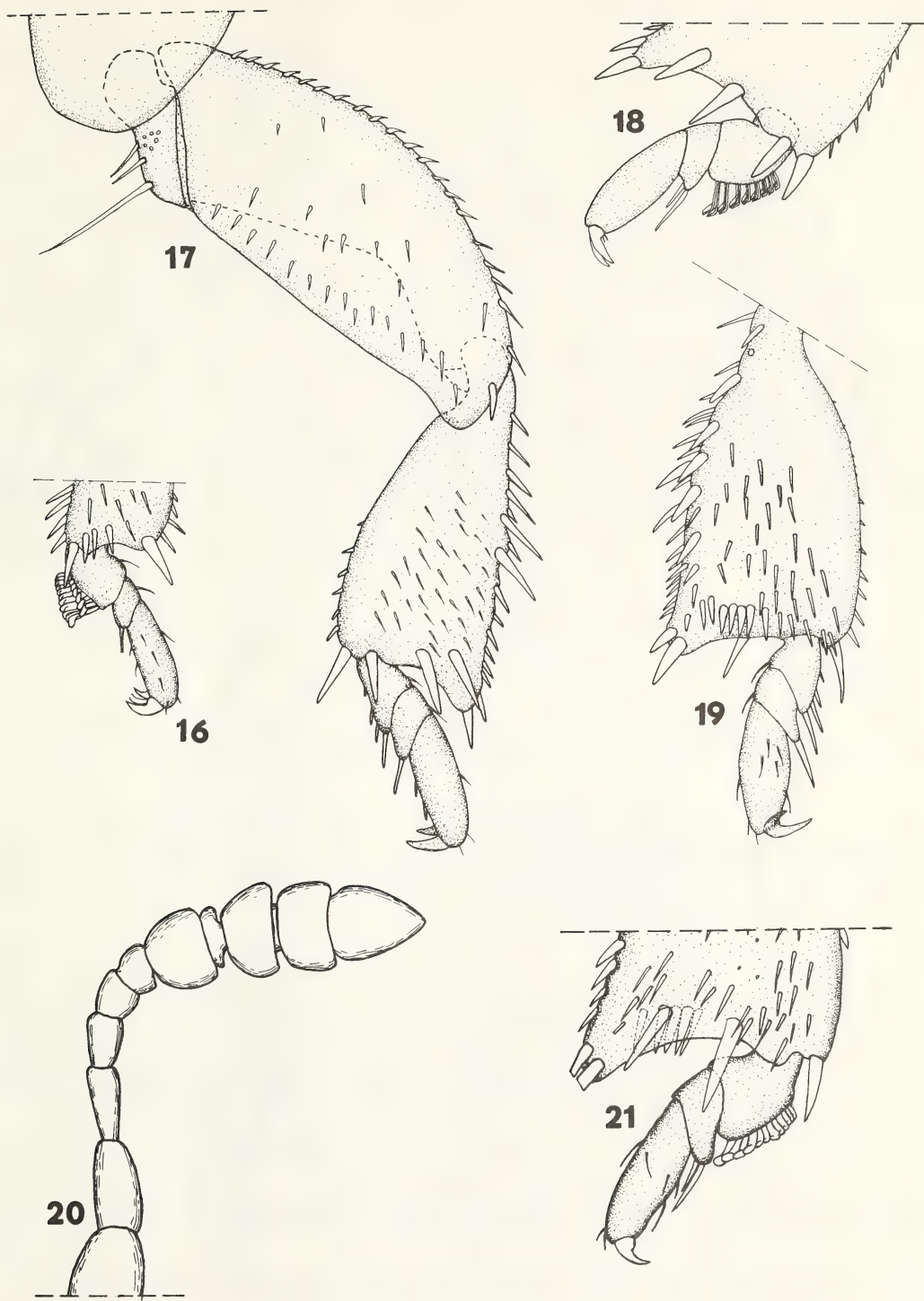
Creagrophorus bihamatus Matthews, 1888: 84.

Lectotype. – Male, BMNH, here designated (examined).

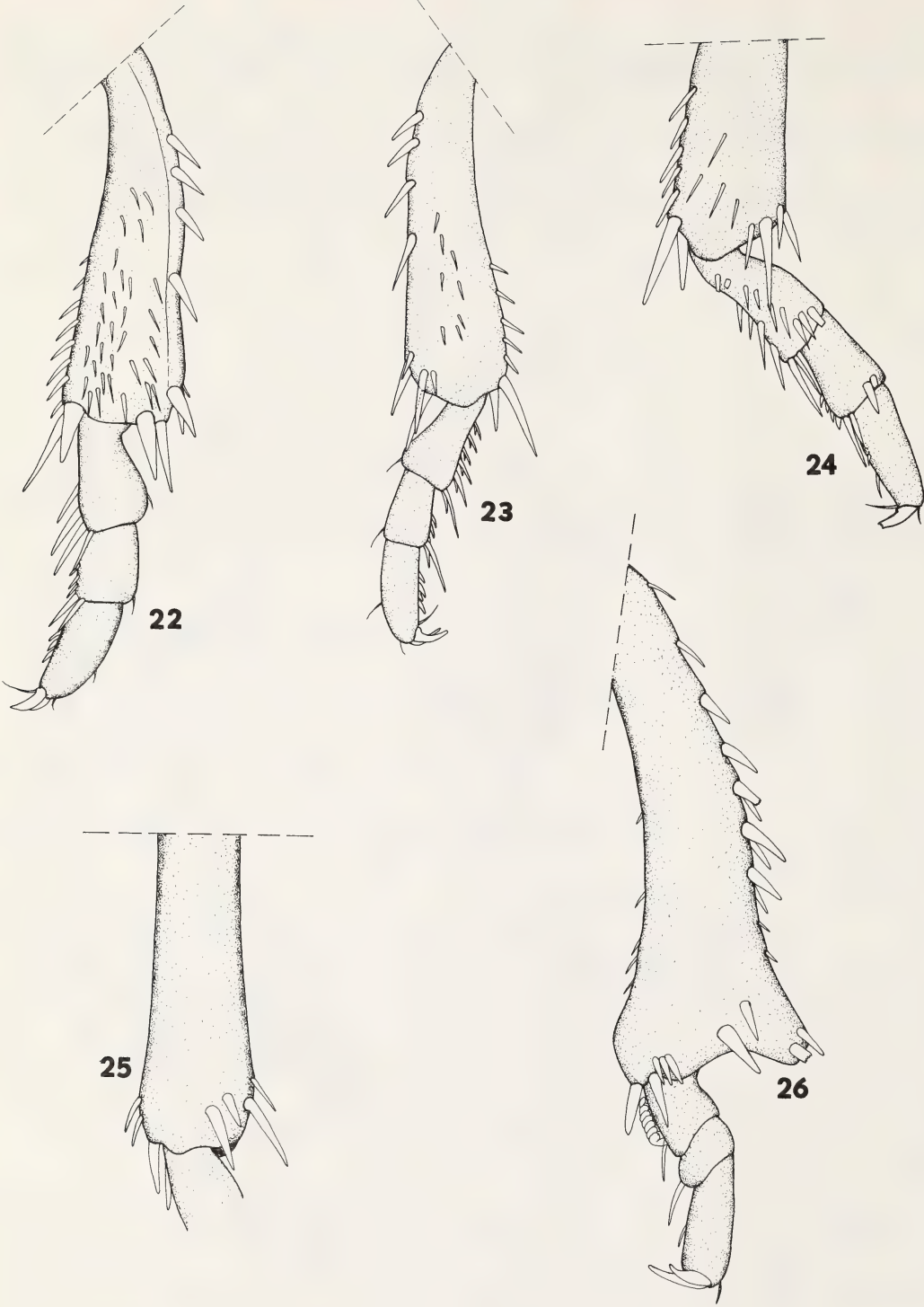
Type locality. – PANAMA, Chiriqui Province, Volcan de Chiriqui.

Diagnostic combination. – Color reddish-brown; male middle femur without hook, hind femur with two hooks (Fig. 14); endophallus with two longitudinal patches of large spines (Fig. 38).

Description. – Length about 2.1 mm.



Figures 16 – 21. *Creagrophorus* spp., legs and antenna: Fig. 16-19, *C. spinaculeus*, Fig. 16, male, front, Fig. 17, female, middle (mesal surface), Fig. 18, male, middle, Fig. 19, female, middle (outer surface); Fig. 20, *C. hamatus*, antenna; Fig. 21, *C. bihamatus*, male, middle.



Figures 22 – 26. *Creagrophorus* spp., legs: Fig. 22-23, *C. spinaculeus*, Fig. 22, male, middle, Fig. 23, female, middle; Fig. 24, *C. bihamatus*, male hind; Fig. 25-26, *C. hamatus*, male, Fig. 25, hind, Fig. 26, middle.

Color. Dark reddish brown, appendages paler.

Microsculpture. Obscure punctules on head, pronotum, and elytra.

Luster. Shining.

Legs. Male middle femur edentate, tibia broad (Fig. 21); hind femur bidentate (Fig. 14), tibia slightly wider apically (Fig. 24).

Male genitalia. Median lobe ventrally curved (Fig. 47), narrowed apically (Fig. 48). Paramere short, broad, not fused (Fig. 49). Endophallus with generally distributed small spines, and two distal, longitudinal patches of larger spines (Fig. 38).

Female. I tentatively accept the female specimen in the BMNH, identified by Matthews, as a member of this species. The middle tibia is widened only apically, the micropunctules are more distinct, and the color paler than the lectotype.

Geographic relationships. – This species occurs at Volcan de Chiriqui in Chiriqui Province, Panama. Matthews also reported *C. hamatus* from this locality.

Cladistic relationships. – *C. bihamatus* is the sister species of *C. spinaculeus*. Synapotypic occurrence of patches of large spines on the endophallus suggest this arrangement.

Material examined. – Type specimens, 1 male, 1 female, only. Lectotype male labelled: SYNTYPE (circular, ringed with blue); *Bihamatus* M. (hand-written); Sp. figured; V. de Chiriqui below 4,000 ft., Champion; B.C.A., Col., II, I. In this specimen the legs on the right side are detached, on the left side they are in position (handwritten); *Creagrophorus bihamatus* M. ♂, det. Hlisenkovsky 1962; *Creagrophorus bihamatus*, M.E. Bacchus det 1978, SYNTYPE; and my lectotype labels. Female specimen (BMNH), also from Chiriqui, also figured in B.C.A.

Creagrophorus jamaicensis Peck

(Fig. 37, 44-46, 69)

Creagrophorus jamaicensis Peck, 1972: 56; Peck, 1977a.

Holotype. – Male, Illinois Natural History Survey, original designation (Peck, 1972) (Not examined).

Type locality. – JAMAICA, St. Andrew Parish, Hermitage Dam.

Diagnostic combination. – Color reddish-brown, luster slightly iridescent; elytral punctules indistinct; middle femur without hook; male hind femur with two hooks; endophallus with small spines, generally distributed, lacking patches of large spines (Fig. 37); Jamaican distribution.

Description. – Length about 1.2–1.4 mm.

Color. Reddish-brown, antennae paler.

Microsculpture. Punctules obscure on head, pronotum, and elytra.

Luster. Shining; somewhat iridescent.

Legs. Male middle femur without hook, hind femur with two hooks; female femora without hooks; tibiae similar in males and females, middle tibia very wide (see figs. in Peck, 1972), similar to those illustrated for *C. spinaculeus*.

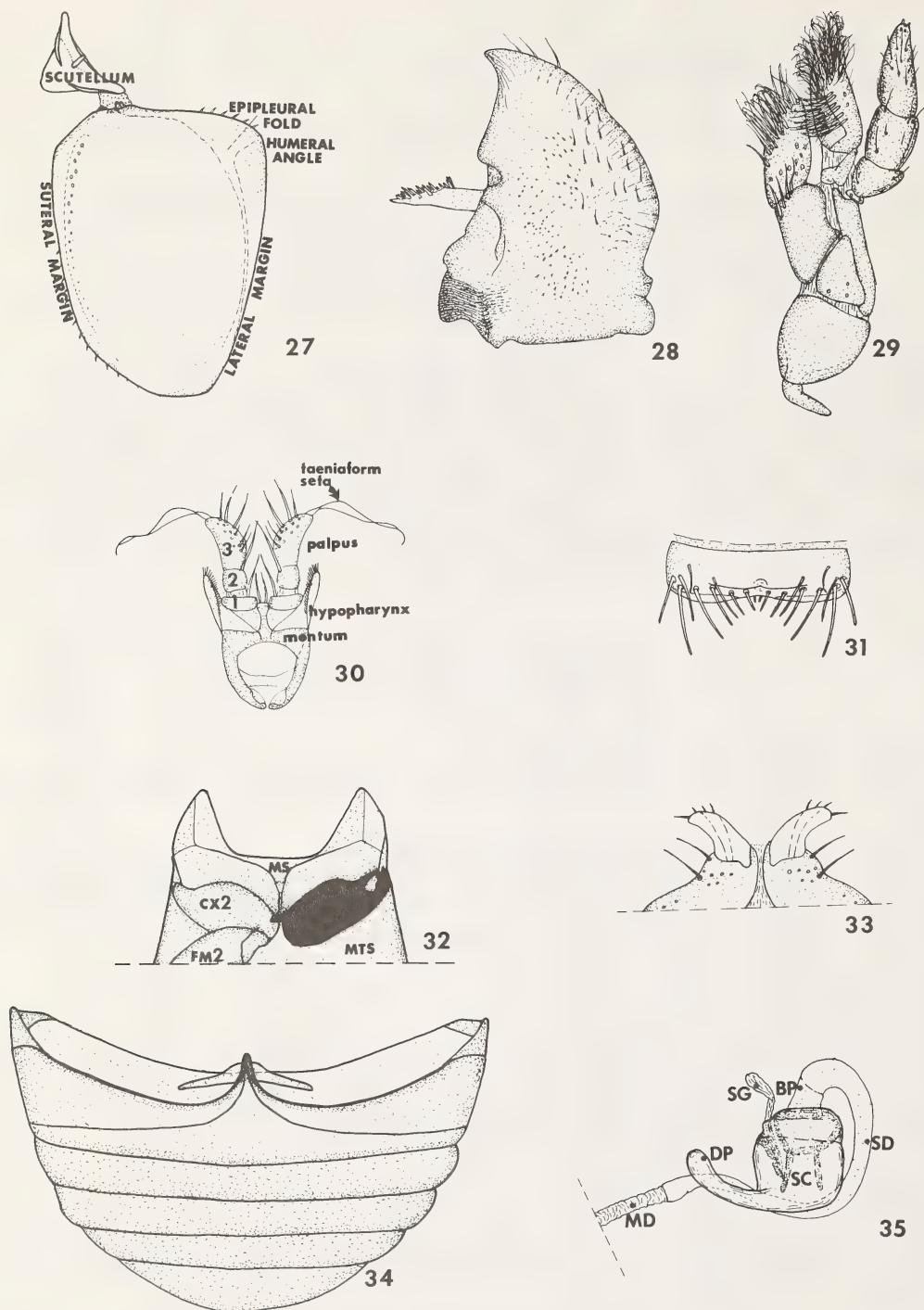
Male genitalia. Median lobe ventrally curved (Fig. 44), apex not fused, narrowed (Fig. 45). Parameres wide (Fig. 46). Endophallus with small spines, irregularly distributed (Fig. 37), without patches of large spines.

Female genitalia. Not examined.

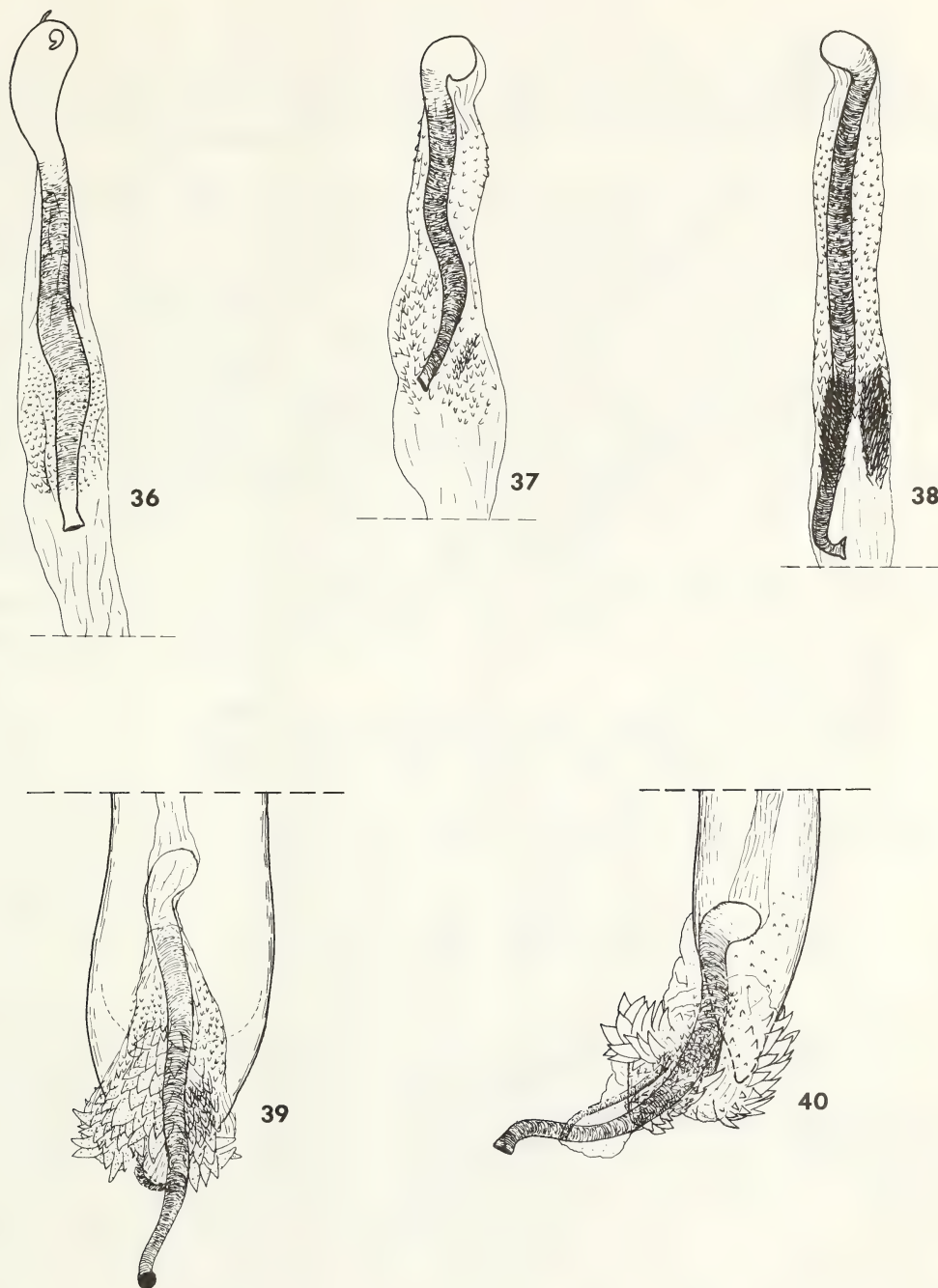
Geographic relationships. – This species is the only one which occurs in the Antilles, and is known only from Jamaica (Peck, 1972; 1977a).

Cladistic relationships. – *C. jamaicensis* is the sister taxon of the *bihamatus-spinaculeus* lineage, based on synapotypic occurrence of two hooks on male hind femur and increased spination of the endophallus.

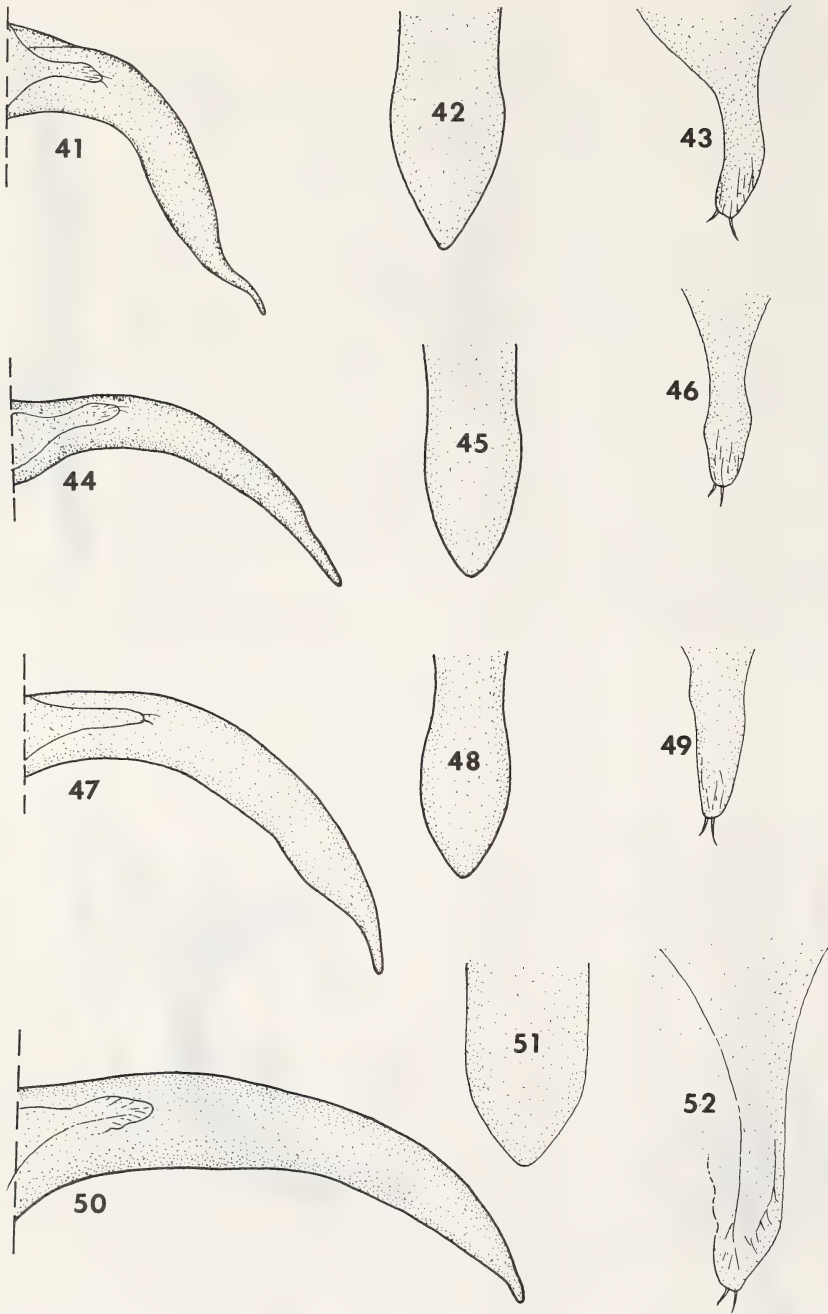
Material examined. – I have seen a female paratype (MCZC) and four specimens from Pt. Antonio, Jamaica (MCZC).



Figures 27 – 35. *C. spinaculeus*: Fig. 27, elytron, dorsal, right; Fig. 28, mandible, right; Fig. 29, maxilla, right; Fig. 30, labium, ventral; Fig. 31, labrum, dorsal; Fig. 32, meso- and meta-sterna; Fig. 33, female genitalia; Fig. 34, female abdomen, ventral; Fig. 35, spermatheca, MD (membranous duct), SD (sclerotized duct), DP (distal process), SG (spermathecal gland), BP (basal process), SC (spermathecal capsule).



Figures 36 – 40. *Creagrophorus* spp., endophallus: Fig. 36, *C. hamatus*; Fig. 37, *C. jamaicensis*; Fig. 38, *C. bihamatus*; Fig. 39-40, *C. spinaculeus*, Fig. 39, ventral; Fig. 40, lateral.



Figures 41 – 52. *Creagrophorus* spp.: Fig. 41-43, *C. spinaculeus*, Fig. 41, median lobe, lateral, Fig. 42, same, apex, ventral, Fig. 43, paramere; Fig. 44-46, *C. jamaicensis*, Fig. 44, median lobe, lateral, Fig. 45, same, apex, ventral, Fig. 46, paramere; Fig. 47-49, *C. bihamatus*, Fig. 47, median lobe, lateral, Fig. 48, same, apex, ventral, Fig. 49, paramere; Fig. 50-52, *C. hamatus*, Fig. 50, median lobe, lateral, Fig. 51, same, apex, ventral, Fig. 52, paramere.

Larvae of *Creagrophorus*

No larvae have previously been described for *Creagrophorus*, or taxa of the *Aglyptinus* association. Information about larvae of Leiodinae has, in general, been sparse and fragmentary (Hatch, 1927; Cornell, 1972). This makes deciding which characters are of value at the genus level problematical, at best.

Leiodid beetles belong to the "Leptinid Association" of families in the Staphylinoidae (Böving & Craighead, 1931; Dybas, 1976). Dybas defined this assemblage of families with the following characters of larvae: (1) denticulate or asperate expanded molar region of mandible; (2) prostheca on inner margin of mandible; (3) urogomphi one or two segmented and articulated; (4) antennae three-segmented, with sensory appendage on segment II; and (5) galea fimbriate. Most of these characters, as pointed out by Dybas, are plesiotypic, but unite several staphylinoid families in a practical sense for purposes of discussion until phylogenetic lines become evident. Dybas (1976) gives the following combination of characters for recognition of leiodid larvae: (1) anal membrane without two prominent claws; (2) epicranial lines present; (3) ocelli present or absent; (4) compound setae often present.

Creagrophorus larvae differ from this typical pattern of characters in the following ways. The mola has distinct transverse grooves, but not distinct teeth or asperites (Fig. 6). The galea is not fimbriate. No distinct epicranial lines are apparent in any of my preparations.

It is not presently clear to me which characters will be of use at the generic level, and which at the species level. Studies of larvae in other genera will eventually make such decisions easier. Meanwhile, only *C. spinaculeus* larvae are available, and are described below.

Creagrophorus spinaculeus new species

(Fig. 6, 53-64; species described above, based on adults)

Diagnostic combination. – Epicranial lines absent (Fig. 54); galea not fimbriate (Fig. 62); four pairs of forked setae on each tergum (Fig. 55) of abdomen; urogomphus segment I quadrisetose, one seta very long, segment II long, crenulate (Fig. 58).

Description. – Late-instar larva (Fig. 53), length about 2.9 mm; width across metathorax about 0.6 mm.

Form. Body subcylindrical in cross-section, widest at metathorax, gradually narrowed posteriorly (Fig. 53).

Color. White to yellowish; mandibles testaceous; more or less distinct brownish spot on each side of midline of abdominal and thoracic terga.

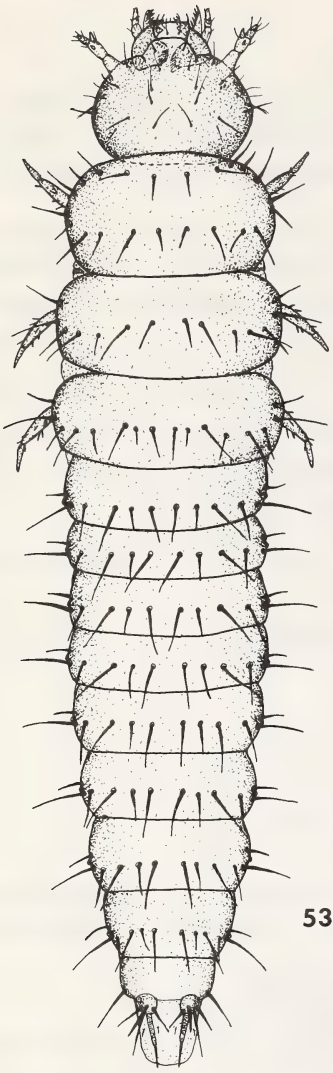
Setae. Forked or simple (pointed).

Sclerotization. Body lightly sclerotized.

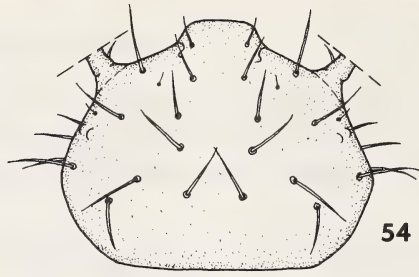
Head capsule (Fig. 54). Without distinct epicranial lines. Clypeus not delimited by suture, except basolateral angles, with single pair of dorsal setae. Labrum (Fig. 60) separated by fine suture; one dorsal pair large setae medially and two pairs minute setae laterally on disc; five pairs of setae along anterior margin, medial pair small. Ocelli, two pairs. Antenna (Fig. 61) with three articles: II long, with large apical sensory appendage and smaller accessory sensory appendage; III with single stout, apical spicule. Maxilla (Fig. 62) with three palpomeres: I large, II much shorter than I, III long, thin with thin walled basal process (digitiform organ) nearly half length of III; galea not fringed (fimbriate); lacinia with comb of five stout setae, apex blade-like (Fig. 63). Labium with two palpomeres; I large, cylindrical, with apicolateral tuft; II much smaller, cylindrical, with apical tuft; ligula broad, apex rounded. Mandibles (Fig. 64) similar, except crenulations distal to median dens on right mandible, absent from left; apex pointed; molar region prominent, with many transverse ridges (Fig. 6); prostheca broad, dentiform.

Thorax. Slightly broader than abdominal segment I, terga not clearly defined. Prothorax with two transverse rows of setae: anterior row entirely of simple (pointed) setae, posterior row with four medial pairs forked setae, one pair of lateral, simple setae. Mesothorax and metathorax each with single row of setae consisting of four medial pairs of forked setae, and single pair lateral simple setae. Mesothoracic spiracle larger than abdominal spiracles, similar in form.

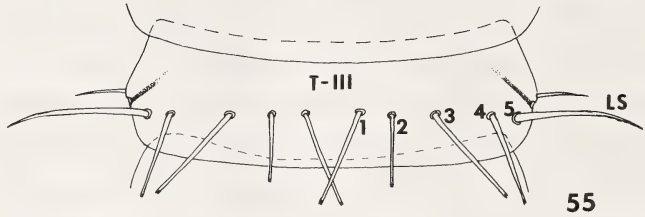
Abdomen. Tergum IX with single pair long, simple, posterolateral setae; all other terga with four pair forked setae, large lateral pair of simple setae, and pair of smaller, simple, post-spiracular setae (Fig. 55). Sterna with three pairs of simple setae each (Fig. 56). Spiracles small, annular, present on segments I-VIII. Urogomphus (Fig. 58) two-segmented: segment I short, wide, quadrisetose, setae simple, one very long (about length of segment II); II long, thin, gradually narrowed, basal three-fourths crenulate ("wrinkled") in



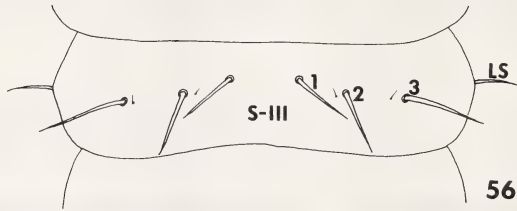
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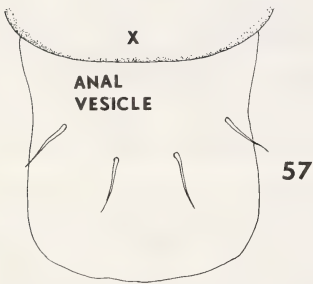
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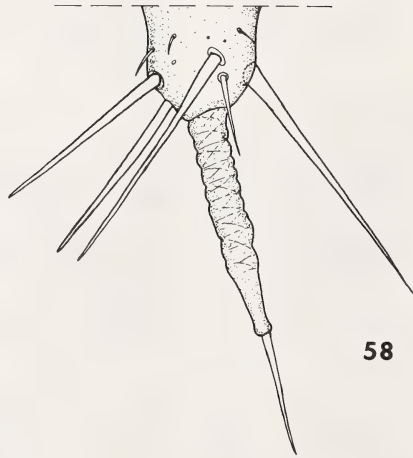
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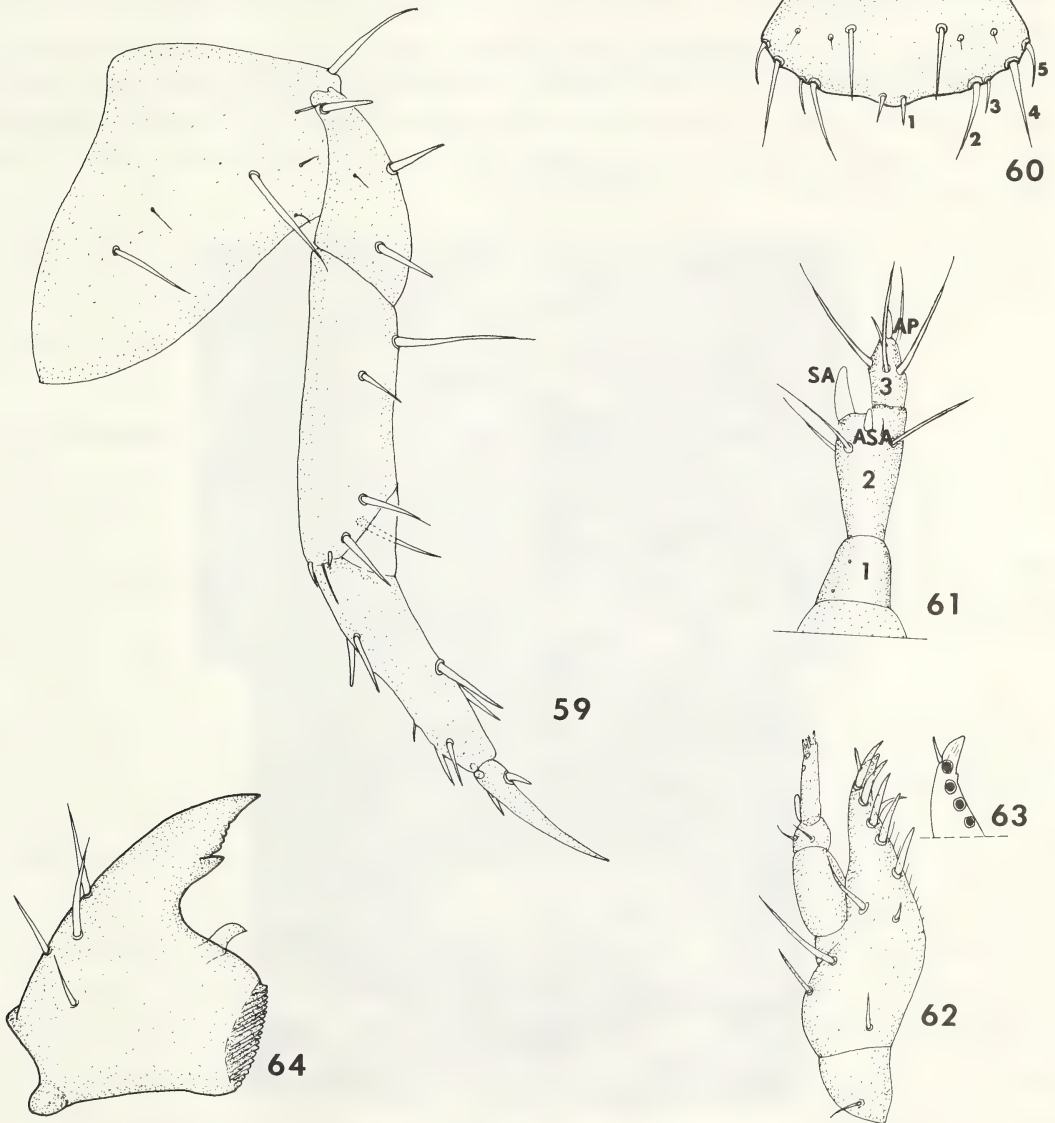
Figures 53 – 58. *C. spinaculeus*, larva: Fig. 53, habitus, dorsal aspect; Fig. 54, head, dorsal aspect; Fig. 55, abdominal tergum III; Fig. 56, abdominal sternum III; Fig. 57, anal vesicle; Fig. 58, urogomphus.

appearance with single, long, apical seta. Anal vesicle with two pairs simple setae (Fig. 57).

Legs. Similar in form to hind leg (Fig. 59).

Material examined. – About 40 larvae were collected with the type series from *Lycogalopsis solmsii* (Gasteromycetes, Lycoperdales, Lycoperdaceae) fruiting bodies in Panama, on Barro Colorado Island. About twelve larvae were deposited in the British Museum (BMNH), and remaining larvae retained in my collection (QDWC).

Comments. Larvae were observed feeding on spores inside puffball fruiting bodies in the field, and “plugs” of spores were visible in larval digestive tracts in slide preparations. No comparative statements are yet appropriate regarding relationships to other leiodids.



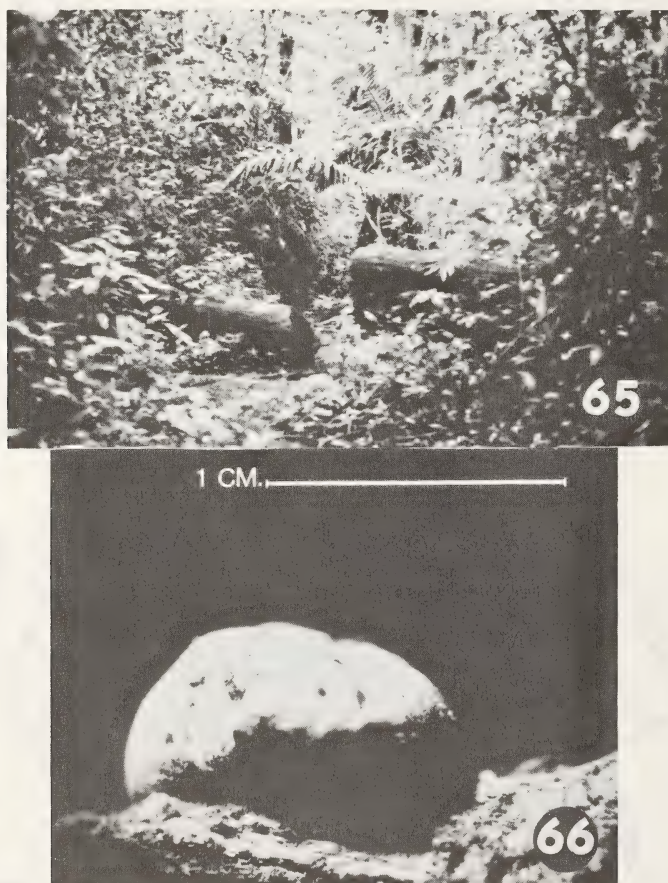
Figures 59 – 64. *C. spinaculeus*, larva: Fig. 59, hind leg; Fig. 60, labrum, dorsal aspect; Fig. 61, antenna; Fig. 62, maxilla; Fig. 63, lacinia apex; Fig. 64, mandible.

ECOLOGICAL RELATIONSHIPS

My only encounter with *Creagrophorus* was in the lowland, tropical forest of Barro Colorado Island (Fig. 65), where both adult and larval *Creagrophorus spinaculeus* were feeding in puffball fruiting bodies (Fig. 66). Although there is no way of estimating the degree of host specificity, as much information as possible about the host should be discussed as a basis for developing explanations for spatial and temporal distribution of *Creagrophorus* beetles.

The host puffball, *Lycogalopsis solmsii* Fisher (Gasteromycetes: Lycoperdales: Lycoperdaceae), is pantropical and recorded from Java (type locality), Congo, Ceylon, Japan, Puerto Rico, Martinique, and Panama. Ligneous substrata seem to be preferred, as is generally true of puffballs (Bessey, 1950; Smith, 1951; Dring, 1973).

Lycogalopsis solmsii was collected previously on Barro Colorado Island and in Balboa, both in the Canal Zone of Panama (Martin, 1939). Abundance of its fruiting bodies was recorded in Balboa during the rainy summer of 1935, but was not noticed during the drier summer of 1937. Smaller series were taken from decaying wood on Barro Colorado Island during both of those years. Moisture seems to be an important parameter for the life cycle of *Lycogalopsis*.



Figures 65 – 66. Habitat and host of *C. spinaculeus*: Fig. 65, lowland tropical forest, Barro Colorado Island; Fig. 66, fruiting body, *Lycogalopsis solmsii* (Gasteromycetes: Lycoperdales).

Larvae were found associated with the fruiting bodies in the field, and extracted by hand in the laboratory. Both larvae and large series of fully-pigmented adults fulfill the criteria established by Lawrence (1971, 1973) for recognition of valid breeding records for fungus beetles (ciids in particular).

Perhaps we can explain the absence of *Creagrophorus* from extensive leaf litter samples taken in Jamaica by Peck (1977a), if *Lycogalopsis* is fairly restricted to ligneous substrata, primarily decaying wood. It will be of great interest to collect specifically for both *Lycogalopsis* and puffballs generally to find if this is true, and what the range of acceptable hosts are for *Creagrophorus*.

Mycologists generally believe that the Gasteromycetes are closely related to (and in fact, are descendants of) the Hymenomycetes (e.g., mushrooms and related fungi). It is not difficult to imagine an *Aglyptinus*-like ancestor, already feeding on Hymenomycetes, adapting to puffball hosts.

Voucher specimens of the host fruiting bodies (*Lycogalopsis solmsii*), identified by Alexander H. Smith, have been deposited in the National Museum of Natural History (USNM) along with the type series of *C. spinaculeus*.

CLADISTICS

Cladistics are used as a method of approximate reconstruction of evolutionary pathways, as in an earlier paper (Wheeler, 1979). Character polarity determinations were based on out-group comparisons with *Aglyptinus* association taxa. Numbers in parentheses refer to characters in Table 2; references to illustrations are given in the table.

Character polarity (Table 2)

Compact structure of the antennal club (15) is interpreted as synapotypic for *Creagrophorus* and Scotocryptini. Similar compaction of clubs occurs in other Leiodini genera (ie., *Isoplastus*, *Apheloplastus* etc.), but I believe it is independently acquired within the *Aglyptinus* association. Eventually, intensive out-group comparisons will refine this and similar questions. The broad, flattened, curved palpomere segment III (1) of the *Creagrophorus* labium is autapotypic for the genus; *Aglyptinus* and Scotocryptini have segment III short, subcylindrical, and more or less truncate apically (the plesiotypic homologue). The taeniaform seta (2) is unique to *Creagrophorus*.

Oblique lines on abdominal sternum III (11) are synapotypic for *Creagrophorus*, *Aglyptinus*, and Scotocryptini. In general, larger body size seems typical of 'primitive' *Creagrophorus* (e.g., *C. hamatus*), and *Aglyptinus* and Scotocryptini, suggesting that smaller size (19) is apotypic for some *Creagrophorus* species. Black coloration (20) of *C. spinaculeus* contrasts with the usual reddish-brown color of *Aglyptinus* association beetles. Elytral punctation is plesiotypic in relation to the *Aglyptinus* association and Leiodini as a whole, and reduction or absence (21) is presumably apotypic. Iridescence (22) is only known in one species of *Creagrophorus* (*C. jamaicensis*). Nature of this iridescence has not been determined, but it subjectively looks different than surface gratings which occur in *Aglyptinus* sp. which will be discussed elsewhere, and is therefore interpreted as autapotypic. Hind femur hooks (8) are autapotypic for *Creagrophorus*, as are middle femur hooks for *C. hamatus* (18). 3-3-3 tarsi (12) are apparently confined to *Aglyptinus* association genera. Compact, subcylindrical tarsi (14) are shared by *Creagrophorus* and *Scotocryptus*. Expansion of the middle tibia is apotypic for *Creagrophorus*. Greater degree of expansion (29) is synapotypic in members of the *jamaicensis-bihamatus-spinaculeus* lineage.

Genital structural information is fragmentary for the out-group; that which is published is not detailed enough for evaluation here (e.g., Hlisnikovsky, 1964). I interpret available data as follows. Annulae of most of the distal portion of the flagellum of the endophallus (3) is autapotypic for

Table 2. Polarity of character states in *Creagrophorus* Matthews and related genera

No.	Character	Plesiotypic state	Apotypic state
1	Palpomere III, labial palpus	Cylindrical, truncate	Wide, flattened, curved (Fig. 30)
2	Taeniaiform seta, labial palpus	Absent	Present (Fig. 30)
3	Flagellum of endophallus	Annulae absent or basal	Annulae distal (Figs. 36–40)
4	Spines of endophallus	Absent	Present
5	Article I, urogomphus	?	With four spines (Fig. 58)
6	Epicranial lines	Present	Absent (Fig. 54)
7	Galea	Fimbriate	Not fimbriate (Fig. 62)
8	Metafemoral hooks	Absent	Present (Fig. 12, 13)
9	Coxites	Long, digitiform	Short, transverse (Fig. 33)
10	Styli	Short, digitiform, lightly sclerotized	Short, wide, curved, highly sclerotized (Fig. 33)
11	Sternum III, oblique lines	Absent	Present (Fig. 34)
12	Tarsi	Formula greater than 3-3-3	Formula 3-3-3
13	Middle tibia	Slender	Expanded (Fig. 25, 26)
14	Tarsi, form	Long, thin	Compact, subcylindrical (Fig. 17)
15	Antennal club, form	Loose	Compact (Fig. 3, 5)
16	Ecological relationship	Hymenomycete feeder (?)	Gasteromycete feeder
17	Ecological relationship	Hymenomycete feeder (?)	Meliponinae bee inquiline
18	Mesofemoral hook	Absent	Present (Fig. 11)
19	Size	Larger	Smaller
20	Color	Reddish-brown	Black
21	Punctuation, elytral	Present	Absent
22	Iridescence, elytral	Absent	Present (faint)
23	Parameres	Freely articulated	Fused to median lobe, in part (Fig. 50)
24	Endophallus patches of spines	Absent (Fig. 37)	Present (Fig. 38)
25	Endophallus patches of spines	Smaller (Fig. 38)	Larger (Fig. 39, 40)
26	Median lobe	Ventrally curved (Fig. 44)	Dorsally curved over apex (Fig. 41)
27	Metafemur, male	With one hook (Fig. 12)	With 2 hooks (Fig. 13)
28	Endophallus spines	Confined to middle (Fig. 36)	More extensive (Fig. 37–40)
29	Middle tibia	Slightly expanded (Fig. 25,26)	Greatly expanded (Fig. 17)

Creagrophorus; annulae are absent from or confined to the basal portion of the flagellum in other *Aglyptinus* association taxa. Evident, broad spines of the endophallus (4) have so far only been seen in *Creagrophorus*, within which a transformational series exists. The trend is toward increased number and size of spines. *C. hamatus* is plesiotypic with only a few spines confined to middle of endophallus (Fig. 36); *C. jamaicensis* has increased numbers of spines (28); *C. bihamatus* and *C. spinaculeus* share synapotypic patches of spines (24); and spines of the patches are increased in size (25) in *C. spinaculeus*. Parameres are partially fused to the median lobe (23) in *C. hamatus*; the plesiotypic homologue is freely articulated parameres in related in-group and out-group taxa. Dorsal curvature of the median lobe (26) is unique to *C. spinaculeus* within the genus.

Transverse, short coxites (9) and flattened, short, highly sclerotized styli (10) of the female genitalia

are autapotypic for *Creagrophorus*. The plesiotypic homologue for both characters involve long, lightly sclerotized, digitiform shaped structures in *Aglyptinus*, *Scotocryptus*, and Leiodinae in general.

Epicranial lines of the larval cranium seem plesiotypic in Staphyloidea and the "Leptinid association" of families (Dybas, 1976), and have been seen in larvae identified as *Aglyptinus* and *Anistoma* (tribe Agathidiini) by me. Absence of the lines (6) from *Creagrophorus* is therefore inferred to be autapotypic. Similarly, lack of fimbriae from larval galeae (7) seems autapotypic (and was seen in the same taxa mentioned above). I suggest that the quadrisetose Article I of the urogomphus (5) may be autapotypic for *Creagrophorus* as well.

Based on observations in the field of North and Middle American species of *Aglyptinus*, I believe that the general (and plesiotypic) ecological relationship involves feeding on various fleshy hymenomycete fungi (mushrooms, etc.). Gasteromycete association in *Creagrophorus* (with *Lycogalopsis*) (16) is autapotypic, as is the inquilinism in meliponine bee nests for Scotocryptini (17).

Cladistic relationships

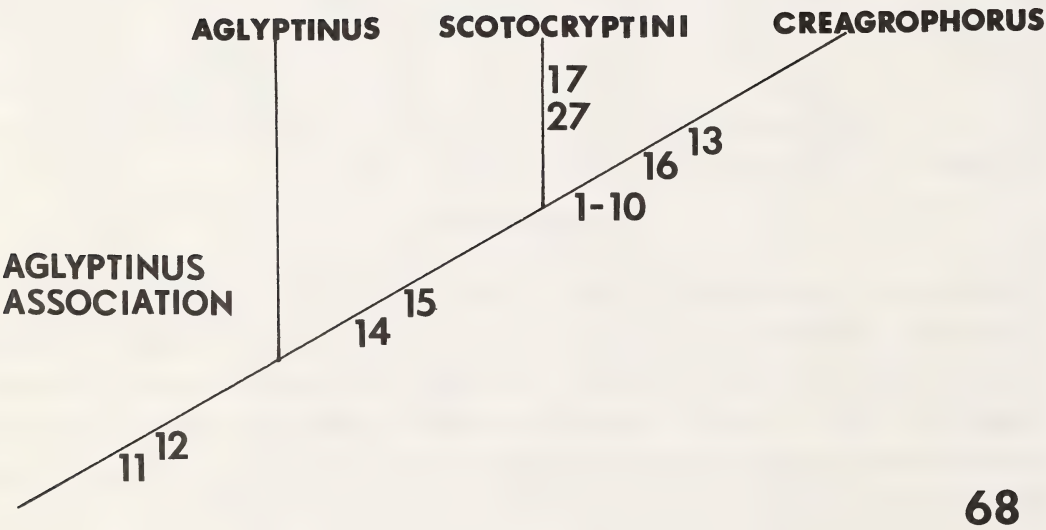
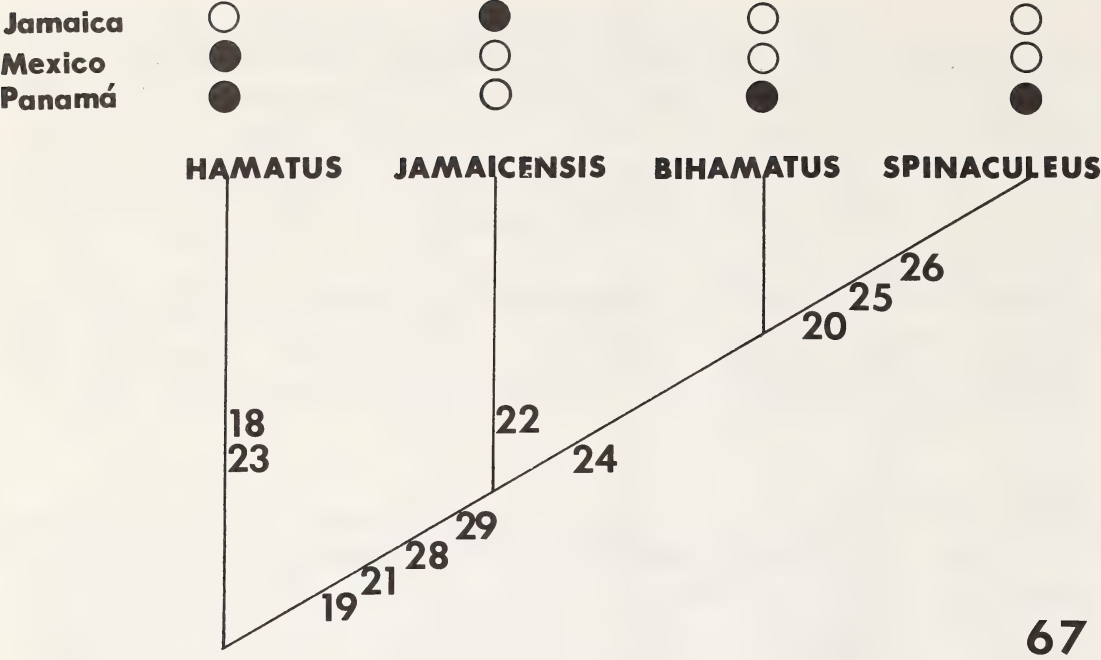
Suprageneric relationships (Fig. 68). – *Aglyptinus* association genera share synapotypic 3-3-3 tarsi (12), and oblique lines on abdominal sternum III (11). The sister group has not been identified, but will probably belong to the Leiodini *sensu stricto* (Jeannel, 1962). Compact tarsi (14) and antennal club (15) support *Creagrophorus*-Scotocryptini as a sister group pair. Their collective sister group is *Aglyptinus*, though monophyly has not been shown for that genus. Transitions to puffball feeding (16) in *Creagrophorus* and inquilinism (17) with bees in Scotocryptini are not yet understood, and a simple dichotomy subjectively seems simplistic in explaining the known extant fauna.

Autapotypic support for monophyletic status of *Creagrophorus* is abundant, including modifications of labial palpi (1,2), endophallus (3,4), female genitalia (9,10), legs (8,13), larvae (5,6,7) and ecological relationships (16).

Intragenetic relationships (Fig. 67). – Fused parameres (23) and a hook on the middle femur of the male (18) are autapotypic for *C. hamatus*. Support for the sister lineage, *jamaicensis-bihamatus-spinaculeus*, includes increased complexity of endophallus spines (28), reduced elytral punctation (21), smaller body size (19), and greatly expanded middle tibiae (29). *C. jamaicensis* is autapotypically iridescent (22). Support for the sister lineage, *bihamatus-spinaculeus*, includes patches of large spines on the endophallus (24). Autapotypies for *C. spinaculeus* are its black coloration (20), dorsally curved median lobe (26), and large endophallus spines (25).

ZOOGEOGRAPHY

Few specimens and sparse locality information strictly limit discussions of both extant zoogeographic patterns and historical explanations for them. I concur with Whitehead (1972) and Ball (1975) who advocate provision of a theoretical basis for additional research, in the form of testable hypotheses, in every systematic study. I feel this is particularly true during early studies of a taxon, such as this one of *Creagrophorus*. General improvement in our understanding of evolutionary patterns will only come about with concern for forming and testing hypotheses, and dismissal of fears about invalidation of our ideas, as discussed by Ball (1978). It is in this spirit that I offer some interpretations of the available zoogeographic data for *Creagrophorus* and related genera.



Figures 67 – 68. Cladograms, numbers refer to Table 2: Fig. 67, intragenetic relationships of *Creagrophorus*; Fig. 68, intergeneric relationships of *Aglyptinus* association taxa.

Distribution patterns

For reasons discussed under 'Speciation patterns' below, I believe that species of *Creagrophorus* are continental in their pattern of species differentiation. I assume that species are widely distributed in suitable habitats, and that endemic populations are not common.

C. hamatus occurs in Mexico (Puebla), and was reported from Volcan de Chiriqui by Matthews (1888). I could not locate the latter specimen, but provisionally accept Matthews' identification as valid. Remaining species constitute the sister-group of *C. hamatus*. *C. jamaicensis* occurs in Jamaica, and the *bihamatus-spinaculeus* lineage in Panama. *C. bihamatus* is known only from the Volcan de Chiriqui area and *C. spinaculeus* from Barro Colorado Island, Canal Zone. Collectively, the distribution of *Creagrophorus* is Middle America, extending northward into Mexico.

Scotocryptini, sister group of *Creagrophorus* is primarily South American, with a northern subtraction pattern (Table 1). Only one species (*Parabystus inquilinus*, see Hatch, 1929b) occurring north of South America does not also have populations in South America. I suggest that this one will also represent a range extension by a South American form, or that its sister species will be South American. Scotocryptines contrast sharply with the ecological relationships of *Creagrophorus*, with their inquiline habits in Meliponinae bee nests.

Speciation patterns

Whitehead (1976) discussed criteria by which two generally distinct patterns of species differentiation may be recognized: continental and islandic. Briefly, clues for recognizing these patterns are as follows.

A. Islandic speciation pattern:

1. High-altitude distributions, generally;
2. Disjunct (differentiated) populations including mountaintops, caves, water-locked islands, etc.;
3. Low-altitude distributions of organisms which are ecologically specialized or habitat-restricted.

B. Continental speciation pattern:

1. Low-altitude distributions, generally;
2. Continuous (undifferentiated) populations including riparian forms along streams, lowland forest forms, etc., characterized by wide geographic ranges;
3. Ecological generalists or non-habitat-restricted organisms.

Whitehead stressed that these are only generalizations of patterns, and that every organism must be evaluated individually. Those found to conform to the islandic pattern are more likely to have been influenced by cyclic weathering of the Pleistocene than continental forms, and hence often evolve at a more rapid rate. How should the speciation pattern be interpreted in *Creagrophorus*?

At first glance, puffball feeding appears to be a rather specialized ecological relationship. Host fungi, however, are typically cosmopolitan (or in the case of *Lycogalopsis*, pantropical) within suitable climatic regions, and occur spottily over wide geographic ranges, presumably occupied by *Creagrophorus*. Fully winged adult beetles undoubtedly spend much of their time migrating from one fruiting body to another in the lowland forest, wherever microclimatic conditions permit successful growth of the host. Thus, we can assume that they have escaped major pressures from Pleistocene cyclic climatic changes, for reasons enumerated by Whitehead (1976) for lowland, tropical, terrestrial carabids, and they should be classified as demonstrating the continental speciation pattern.

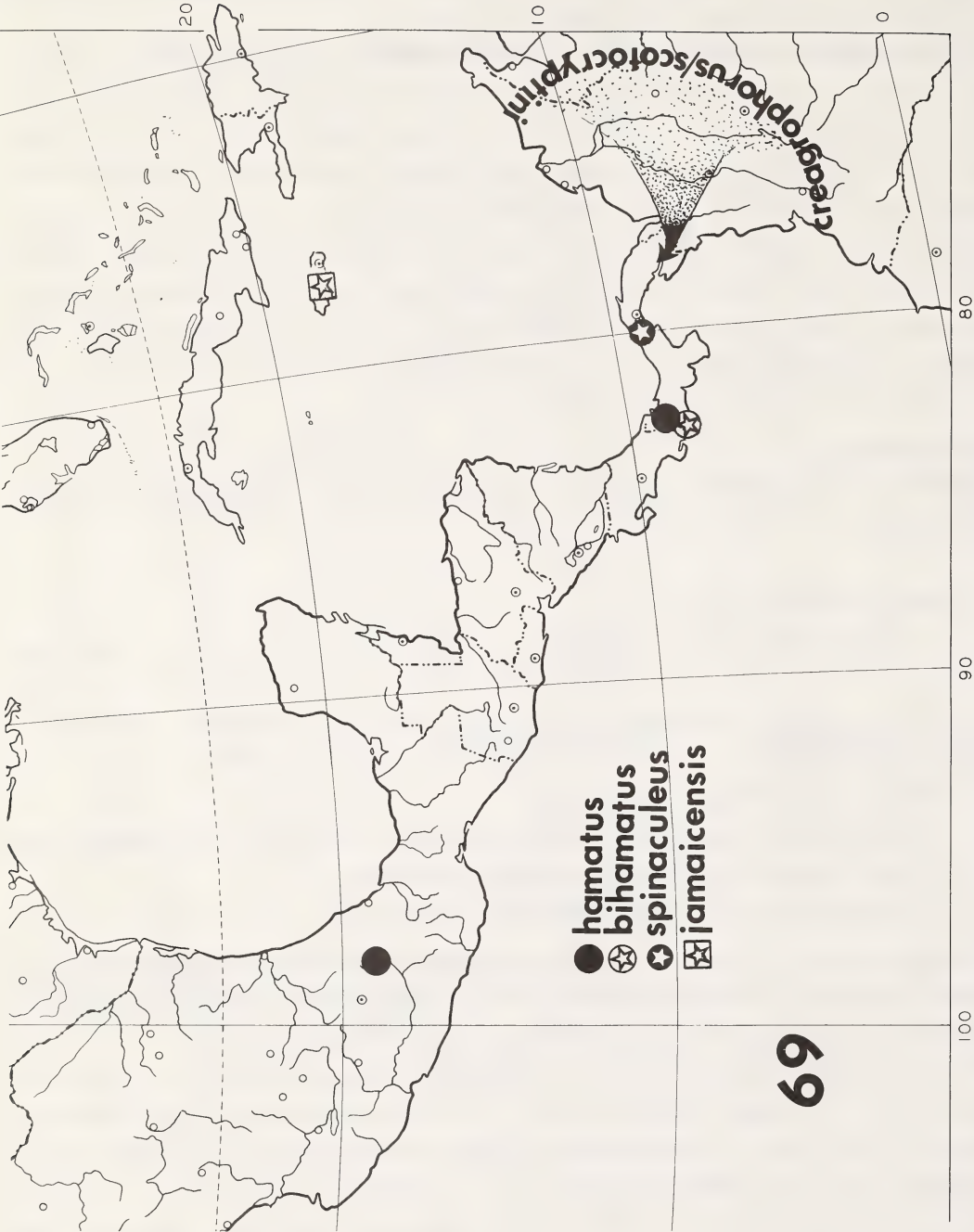


Figure 69. Geographic distribution of species of *Creagrophorus*, and South American ancestral origin.

Historical zoogeography

Vicariance biogeography (see Platnick & Nelson, 1978; Rosen, 1978; Croizat *et al.*, 1974) provides a means of estimating recency of common ancestral ranges from knowledge about cladistic relationships. Congruence of a number of vicariant sister pairs may indicate a general track, which can potentially be causally explained through historical geologic events.

Constraints imposed by lack of empirical data about *Creagrophorus* geographic distribution preclude detailed vicariant hypotheses (ie., those correlating *Creagrophorus* vicariant events with those of other groups, and with known geological events). Albeit, I believe that it would be useful to discuss the general sequence of vicariant events indicated by present data. Tests and substantiation of these ideas would make more detailed biogeographic analyses possible.

Historical scenario. – Ancestral *Creagrophorus* entered Middle America from South America (Fig. 69), became widespread, and differentiated from the southern ancestral stock which is today represented by Scotocryptini. The scotocryptines have become specialized for inquilinism in Meliponinae bee nests. The first vicariant event isolated the *hamatus* lineage to the north of the Tehuantepec portal. The second was a division of nuclear Middle American and southern Middle American stocks (the nuclear stock dispersed to Jamaica). The third vicariant event isolated sister species to the north and south of the Chiriqui volcanic region (*bihamatus* to the north, *spinaculeus* to the south).

Predictions. – Any discussion about zoogeography at this early date in studies of *Creagrophorus* is meaningless without some obvious utility to later research. Therefore, I offer the following predictions as a framework for continued study.

1. Species conform to a continental pattern, enjoying wide geographic ranges.
2. If *C. hamatus* is actually widespread, no additional species of the *hamatus* lineage will be found which have originated in Middle America and/or are adapted to the same hosts.
3. The *jamaicensis* lineage is represented in nuclear Middle America by either *C. jamaicensis* itself or its sister species. If *C. jamaicensis* has mainland populations, then no additional species is predicted. Similarly, if *C. jamaicensis* is widespread in the Antilles, no other insular members of the *jamaicensis* lineage are expected.
4. *C. bihamatus* occurs throughout southern Middle America, north of Chiriqui. Absence of this a species from nuclear Middle America is a corollary of the presence of a member of the *jamaicensis* lineage there in prediction 3.
5. *C. spinaculeus* is the southern vicariant of the Chiriqui barrier. It is either allopatric or parapatric with *C. bihamatus*.
6. *C. bihamatus* and *C. spinaculeus* actually share a most recent common ancestor (ie., no additional species of the *bihamatus-spinaculeus* lineage exist).
7. The sequence of vicariant events hypothesized above require that no additional branching points exist on the lineage leading to *bihamatus-spinaculeus*. Specifically, the *jamaicensis* lineage is the sister of the *bihamatus-spinaculeus* lineage, and the *hamatus* lineage sister to these collectively.
8. *Creagrophorus* is absent from South America. If any species do exist there, they will not be part of the Middle American lineage.

Some aspects of the historical scenario and the predictions are bold extrapolations from a limited amount of empirical data. My intent is to set forth possible explanations for the observed pattern of distribution, which can subsequently be field-tested and supported or rejected. The eventual outcome should be the same: approximation of the actual sequence of events leading to present *Creagrophorus* patterns. These ideas will minimally serve as a template for arranging later observations and a stimulus

to continued field work in puffball/leiodid beetle relationships.

CONCLUSIONS

Many conclusions have been reached in this study which are stated or implied within the text. It would be useful, however, to draw some conclusions of a general nature from the study as a whole. There remains much to be done in the field before ideas about ecological and zoogeographic relationships of *Creagrophorus* beetles become stable. I hope that this study has set the stage for such investigations. I urge detailed study of the Scotocryptini, and suspect that the tribal status must be abandoned, based on my cladistic analysis. My discussion of the larvae is a minor contribution to an area of study in the Leiodinae which is virtually untouched. Ecological data, though limited, should now be sufficient to allow (and stimulate) the accumulation of specimens and information about hosts and geographic distributions throughout Middle America.

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CORRIGENDA — *Quaestiones Entomologicae*, Volume 15(3)**Straneo — Classification of South American Pterostichini****page/line**

355/ 6 remove “Cephalostrichus Straneo”

355/35 change “Cephalostichus Straneo, 349, 353” to “Cephalostichus Straneo, 345, 349, 353”

Kurtak — Seasonal changes in larval black fly food**page/line**

358/16 change “Naumann” to “Neeley”

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